



# Task-partitioning in insect societies: Non-random direct material transfers affect both colony efficiency and information flow

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## HIGHLIGHTS

- ▶ We model task-partitioning in insect colonies based on non-random interactions.
- ▶ We test how 2 different mechanisms generating non-random interactions affect colony efficiency.
- ▶ We find that non-random interactions affect the time delays experienced by workers waiting for a transfer partner.
- ▶ Non-random interactions also affect the information transfer during task-partitioning.

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## ABSTRACT

Task-partitioning is an important organisational principle in insect colonies and is thought to increase colony efficiency. In task-partitioning, tasks such as the collection of resources are divided into subtasks in which the material is passed from one worker to another. Previous models have assumed that worker–worker interactions are random, but experimental evidence suggests that receivers can have preferences to handle familiar materials. We used an agent-based simulation model to explore how non-random interactions during task-partitioning with direct transfer affect colony work efficiency. Because task-partitioning also allows receivers and donors to acquire foraging related information we analysed the effect of non-random interactions on informative interaction patterns. When receivers non-randomly rejected donors offering certain materials, donors overall experienced increased time delays, hive stay durations and a decreased number of transfer partners. However, the number of transfers was slightly increased, which can improve the acquisition and quality of information for donors. When receivers were non-randomly attracted to donors offering certain materials, donors experienced reduced transfer delays, hive stay durations and an increased number of simultaneous receivers. The number of transfers is slightly decreased. The effects of the two mechanisms “non-random rejection” and “non-random attraction” are biggest if the number of foragers and receivers is balanced. In summary, our results show that colony ergonomics are improved if receivers do not reject donors and if mechanisms exist that help receivers detect potential donors, such as learning the odour of the transferred food. Finally, our simulations suggest that non-random interactions can potentially affect the foraging patterns of colonies in changing environments.

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## 1. Introduction

Social insects often live in highly complex societies where different tasks are performed by different groups of workers.

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In some cases, a single colony can contain millions of highly specialised workers (Wilson, 1971; Hölldobler and Wilson, 2009). An efficient and dynamic regulation of vital tasks such as brood care, nest-defence or foraging is important for the success of colonies. Two key organisational principles are division of labour (DoL; reviewed in Wilson (1971), Hölldobler and Wilson (1990, 2009), Robinson (1992), Beshers and Fewell (2001)) and task-partitioning (reviewed in Ratnieks and Anderson (1999a)). DoL means that different workers specialise on different subsets of tasks. In task partitioning, the tasks themselves are divided into

parts that are performed by different groups of workers. For example, the transport of materials, such as food, is divided into sequential stages in which the material is passed from one worker to another (Ratnieks and Anderson, 1999a). Well studied examples are nest-building in *Polybia occidentalis* wasps, which requires the coordinated action of 3 different types of interacting foragers (Jeanne, 1986), bucket-brigades in leaf foraging leaf-cutter ants (Anderson et al., 2002; Röschard and Roces, 2011, 2003) and nectar/honeydew transfer in many ants, wasps and bees (von Frisch, 1923; Park, 1925; Rösch, 1925; Lindauer, 1948). While liquid materials (e.g. nectar or water) are transferred directly between workers, solid materials (e.g. seeds, leaf fragments or insect prey) are transferred both directly and indirectly, e.g. via a cache (Ratnieks and Anderson, 1999a).

Task-partitioning is taxonomically widespread (Ratnieks and Anderson, 1999a) and appears to be particularly common in advanced, highly eusocial species. Nectar transfer, for example is present in all highly eusocial bees (Apini and Meliponini) studied so far (Hart and Ratnieks, 2002), but not in the primitively eusocial bumble bees (Michener, 1974). It has been suggested that the time-costs of task-partitioning are smaller for larger colony sizes (Anderson and Ratnieks, 1999) that are typical for more advanced societies (Bourke, 1999). A major disadvantage of task partitioning with direct transfer is that it causes time costs because the interacting workers first need to find each other and then transfer material (Ratnieks and Anderson, 1999a; Ratnieks and Anderson, 1999b). On the other hand, task partitioning is assumed to improve colony efficiency, partly because it leads to higher performance of more specialised individual workers, e.g. due to learning (Ratnieks and Anderson, 1999a).

Social insects have evolved ways to acquire additional information via task-partitioning. Wasp and honey bee foragers, for example, acquire information about the balance between collection and processing capacity of the colony from the time they need to find a transfer partner (Jeanne, 1986; Seeley et al., 1991; Seeley, 1989; Seeley and Tovey 1994): if a honey bee forager finds an unloading partner quickly (Lindauer, 1948; Seeley et al., 1991; Seeley, 1989; Seeley and Tovey, 1994; Lindauer, 1954) or has many receivers during unloading (Farina, 2000; De Marco, 2006; Grüter and Farina, 2009) she is more likely to perform a waggle dance to recruit more foragers to her food source. If, on the other hand, a forager experiences difficulties in finding receivers her motivation to recruit drops. In this way, the balance between foragers and processors is maintained in a way that keeps delays at a minimum (Seeley, 1995; Anderson and Ratnieks, 1999). Another advantage of task partitioning in foraging is that receiving workers can gain important foraging related information. Honey bee workers receiving nectar inside the colony, for example, learn the odour of the transferred nectar (von Frisch, 1923; von Frisch, 1967; Gil and De Marco, 2005; Farina et al., 2005; Farina et al., 2007; Grüter et al., 2006). They can store this information in long-term memory (Arenas et al., 2008; Grüter et al., 2009) and use it later in life to find profitable food sources (Arenas et al., 2007, 2008; Balbuena et al., 2012). Hence, task-partitioning affects not only colony work efficiency but also offers opportunities to acquire foraging related information.

An important assumption of previous models exploring the ergonomic and informational consequences of task-partitioning was that interactions between workers of two interacting groups are random (Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999b; Gregson et al., 2003); 'ergonomics' here refers to the performance and efficiency of colonies (Oster and Wilson, 1978). Empirical evidence suggests, however, that this might often not be the case: Goyret and Farina (2005) found that receivers were 6.5 times more likely to unload a forager returning with nectar of a known food-odour than a forager with nectar of a novel odour. In this case, non-randomness is likely to be a

consequence of olfactory learning of food odours (Grüter and Farina, 2009). Individual and social olfactory learning are widespread in social insects (e.g. in ants (Robinson, 1992; Roces, 1990; Provecho and Josens, 2009), wasps (Maschwitz et al., 1974; Jandt and Jeanne, 2005), bumble bees (Dornhaus and Chittka, 1999) or stingless bees (Lindauer and Kerr, 1960; Mc Cabe et al., 2007) and, hence, non-randomness in nectar transfer is potentially common in social insects. More generally, non-random interactions in task-partitioning can be expected whenever a worker has a bias, either acquired or innate, towards or against a particular kind of transferred material, e.g. because of its size, odour or taste.

Here, we developed an agent-based simulation model to explore how non-random interactions affect colony efficiency and information flow in colonies of interacting agents. Non-randomness could be caused by receivers rejecting donors that offer a novel or undesirable type of material (non-random-rejection). Observations in honey bees suggest an additional mechanism. It has been shown that workers are attracted to foragers carrying familiar food odours (Grüter and Farina, 2009; von Frisch, 1967; Balbuena et al., 2012; Grüter et al., 2008; Grüter and Ratnieks, 2011) (non-random-attraction). In this model we tested the effects of these two mechanisms, non-random-rejection and non-random-attraction, on colony efficiency and information flow. In particular, we tested the effects of non-random interactions on the time foragers and receivers need to find a transfer partner (unloading delays), the hive-stay time of foragers, the number of transfers per hive stay needed for complete unloading, the number of unloading partners and the balance between foragers and receivers.

## 2. The agent based simulation model

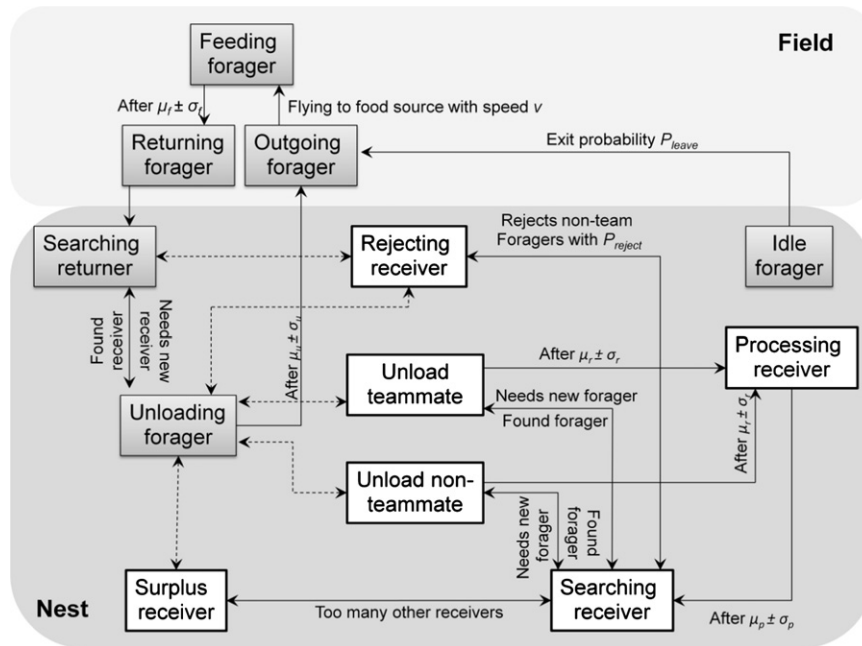
We developed a spatially explicit agent-based model of two types of interacting agents, foragers and receivers, using NetLogo 4.1.2 (Wilensky, 1999) (the NetLogo file can be found in the online material). The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010).

### 2.1. Purpose

The purpose of the model was to explore the effects of non-random interactions between foragers and receivers on colony efficiency and interaction patterns. The model resembles the situation of nectar collection and unloading in honey bees and parameters were taken from the honey bee literature, but the modelled situation is similar to task partitioning of liquid material in many species of ants, social bees and wasps (Ratnieks and Anderson, 1999a).

### 2.2. Entities, state variables and scales

We used a range of agent populations from 8 to 1000, with a default ratio of foragers vs. receivers of 1:1. These colony sizes represent a broad range of species that differ in their forager and food receiver numbers. Since only a minority of workers in a colony are active foragers and receivers, our modelled situation reflects the situation of colonies that are much larger than our actual agent population. Foragers could assume any one of 6 different states (Fig. 1): idle inside the nest, flying to a food patch, feeding at a food patch, returning to the hive, searching for unloading partners, unloading. Food receivers could also assume any of 6 different states (Fig. 1): searching for a donor, unloading from a team member, unloading from a non-team member, surplus receivers (receivers contacting a forager that already unloads to the maximum number



**Fig. 1.** State diagram for the agent-based model. All foragers start as idle foragers; forager-states are indicated by grey boxes. All receivers start as searching receivers; receiver-states are indicated by white boxes. Solid arrows indicate the possible direction of the change in state. Dashed arrows indicate possible interactions between foragers and receivers. See Table 1 for values.

of receivers), receivers rejecting a donor, and full receivers that process food and are unavailable for transfers. In the default situation, agents belonged to one of two teams of equal size. Each team contained an equal number of foragers and receivers. In nature, this corresponds to a colony collecting two different types of food. Honey bee colonies often collect several types of food during a day, but usually only about 5 different types are collected frequently (Free, 1963) and individual foragers usually focus on one particular type of food for up to several days (Ribbands, 1949).

The simulated agents occupied a specific location (off-lattice) at every point in time and were located on a two-dimensional square grid with a circular nest and a food patch at a distance of 45 patches from the nest centre. This corresponds to a nearby food source (flight time of approx. 35 s). Increasing the food distance had the same effect as reducing the proportion of foragers, because foragers spent more time moving between the nest and the food source. The effect of a reduced proportion of foragers was tested separately. The nest had a radius of 11 squares. Varying the nest radius has the same effect as varying the agent number, which was tested separately. The food source had a size of 1 patch.

Simulations were run in discrete time steps ( $t$ ). Model parameters (Table 1) were chosen so that one time step in a simulation corresponds to 1 s. Honey bee foragers show considerable variation in the duration of foraging trips, from a few minutes to more than 1 h (Park, 1926; Butler et al., 1943). Little is known about the duration of food processing of full processors, i.e. the time between filling the crop and returning to the delivery area for the next round of food reception. For simplicity, we chose a default foraging trip duration ( $\mu_f \pm \sigma_f$  [mean  $\pm$  SD]) that equalled the food processing duration ( $\mu_p \pm \sigma_p$ ) (Table 1). This duration was taken from a normal distribution with a mean of 20 min and an SD of 20% of the mean ( $20 \pm 4$  min). Changing these durations had the same effect as changing the relative numbers of foragers and receivers, which was explored separately. Likewise, forager unloading time ( $\mu_u \pm \sigma_u$ ) equalled receiver filling time ( $\mu_r \pm \sigma_r$ ). The default value was  $60 \text{ s} \pm 12 \text{ s}$  (De Marco, 2006; De Marco and Farina, 2003).

**Table 1**

Overview of parameters and values used in the model. Mean  $\pm$  standard deviation is shown.

	Default values	Other values tested
Agent population	8, 20, 100, 400, 1000	24, 96, 384
Number of teams	1, 2	3, 4
Forager feeding time ( $\mu_f \pm \sigma_f$ )	$1200 \pm 240 \text{ s}^{\text{a,b}}$	$2400 \pm 480 \text{ s}$
Forager-unloading-time ( $\mu_u \pm \sigma_u$ )	$60 \pm 12^{\text{c,d}}$	-
Receiver-filling-time ( $\mu_r \pm \sigma_r$ )	$60 \pm 12$	-
Max. simultaneous receivers	$4^{\text{d,e,f}}$	1
Processing duration ( $\mu_p \pm \sigma_p$ )	$1200 \pm 240 \text{ s}$	$2400 \pm 480 \text{ s}$
Walking speed inside nest ( $v_w$ )	0.5 patches/time step	-
Flying speed ( $v_f$ )	1 patch/time step	-
Exit-probability at start ( $P_{\text{leave}}$ )	0.01 per time-step	-
Frustration-time	5 time steps	-
Rejection-time	2 time steps	-
Attraction-radius (patches, $R_{\text{attr}}$ )	0, 0.75, 1.5, 2.25	1
Rejection probability ( $P_{\text{reject}}$ )	0%, 100%	33%, 67%

References used to estimate some of the parameters:

- <sup>a</sup> Park, 1926;
- <sup>b</sup> Butler et al., 1943;
- <sup>c</sup> De Marco and Farina, 2003;
- <sup>d</sup> De Marco, 2006;
- <sup>e</sup> Farina, 1996;
- <sup>f</sup> Farina and Wainseboim, 2001.

Each simulation ran for 36,000 time steps (corresponding to 10 h) in order to allow the system to settle to equilibrium. The first 10,000 time steps were ignored for data collection. Because of the stochastic nature of the model, 30 model runs were performed for each combination of parameter values. We checked the variability between runs (indicated by the standard errors in the figures), to confirm that this number of runs per combination was sufficient.

### 2.3. Process overview and scheduling

Foragers that left the nest flew directly to the food patch, where they spent  $\mu_f \pm \sigma_f$  to collect food (Table 1). Foragers then flew back to the nest and started searching for an available

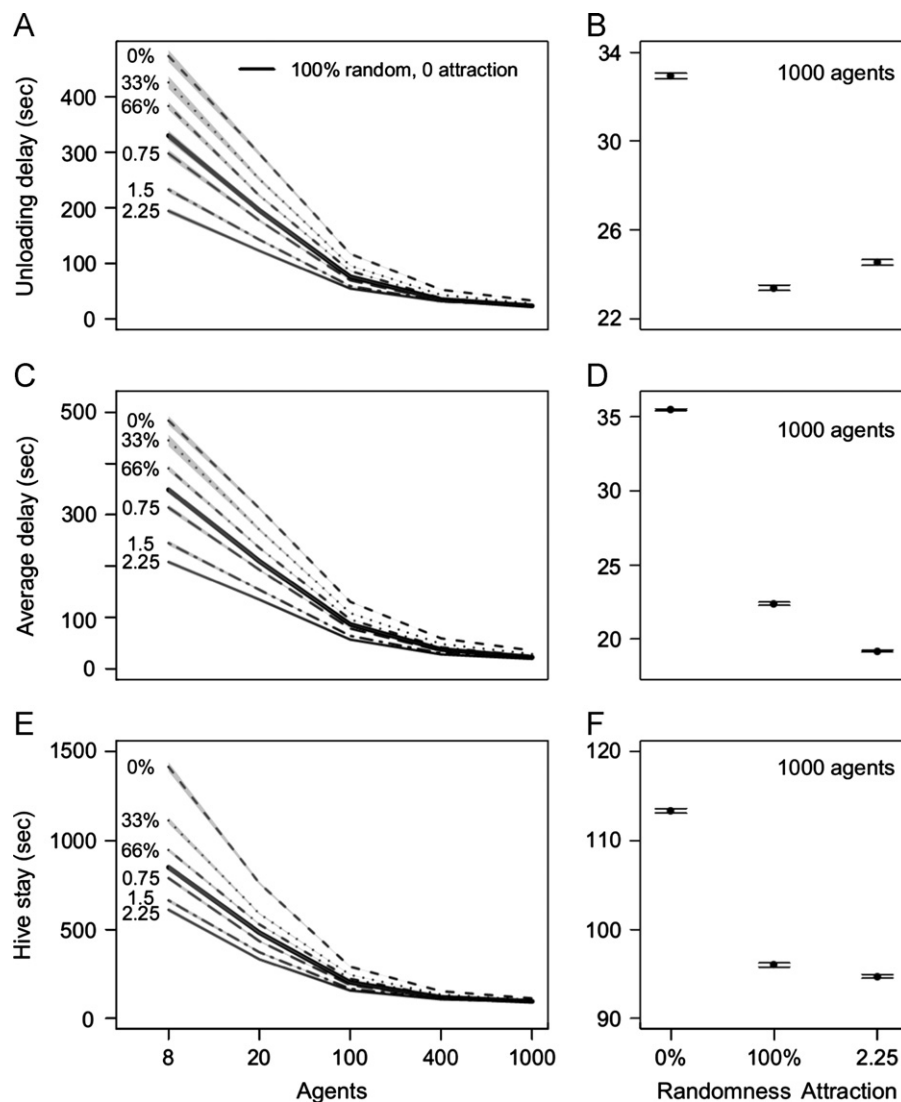
receiver by performing a random walk. If a receiver was full before the forager was empty, the forager performed a random walk until it found another available receiver (Fig. 1). After complete unloading, foragers left the nest and flew back to the food patch.

Receivers performed a random walk inside the nest if they were not engaged in a transfer. When they encountered a returned forager or a transferring forager on their patch they started to receive food. Forager honey bees (and other bees or ants) often transfer to several receivers simultaneously, but rarely more than 4 (De Marco, 2006; Farina, 1996; Farina and Wainelboim, 2001). Therefore, we allowed up to 4 receivers to unload food from the same forager (previous models of task-partitioning allowed only one receiver per forager, e.g. (Anderson and Ratnieks, 1999; Ratnieks and Anderson, 1999b; Gregson et al., 2003)). The amount of food that each unloading receiver obtained depended on the number of simultaneously unloading receivers: the amount of food was divided by the number of simultaneous unloading receivers. This was implemented by advancing a receiver filling timer by  $1/(\text{unloading receivers})$  per time step. For example, if 3 receivers would simultaneously unload a forager, their filling timer would

advance  $1/3$  per time step. For simplicity it is assumed that all unloading receivers receive food at the same rate. If receivers were unable to unload a forager because it was already donating food to 4 other receivers, the receiver (surplus receiver) would perform a random walk for 5 time steps before becoming available again for unloading. If receivers were full, that is their filling timer reached the filling time ( $\mu_r \pm \sigma_r$ ), they became processing receivers. After food processing, receivers started to perform a random walk and search for unloading partners.

We tested 3 different situations: (I) searching receivers randomly unloaded all foragers (complete randomness), (II) receivers rejected (ignored) foragers that were not from the same team with a rejection probability  $P_{\text{reject}}$  (non-random rejection) and (III) receivers unloaded all foragers but recognised foragers belonging to the same team if they were within the attraction-radius  $R_{\text{attr}}$  (non-random attraction) (Table 1). A receiver then walked towards the nearest forager of the same team.

We also tested the three situations when there were 3 or 4 different teams and when the team sizes were unequal. In the latter case, we simulated 3 different teams: 1 large team (team 1: 100 or 1000 agents), one small team (team 2: 20 agents) and a



**Fig. 2.** The effect of non-random interactions on unloading delays, average delays and hive stay time with different colony sizes. The thicker solid line (A, C, E) indicates a situation of completely random interactions and without non-random attraction. The dashed lines above show situations where receivers show varying probabilities to accept non-team foragers (67%, 33% and 0%). The dashed lines below the solid line show situations where receivers show attraction to team-foragers at different distances (0.75, 1.5, 2.25 patches). Figures B, D and F show only the situation with 1000 agents. Standard errors are shown as a grey area.



third team that only consisted of foragers (10 agents). The third team simulated a situation where a small group of foragers discovers a novel food type that is not yet familiar to receivers. Team 2 simulated a situation where there was already a small number of receivers attracted to the new type of food.

#### 2.4. Design concepts

The concepts of adaptation, objectives and prediction are not important in this model. There is no learning in the model. While learning during transfers as a potential cause of non-random interactions is plausible (see Section 1), the purpose of this model was to test the consequences of non-random interactions, not its causes. Sensing is important in this model: receivers searching for unloading partners were able to recognise whether foragers belonged to their own “team” if they were within the attraction-radius (situation III). In situation II, they were able to recognise if a forager on the same patch was not from the same team. Receivers joining the patch of a forager were also able to recognise if there was no available space for an additional receiver because there were already 4 unloading receivers. Foragers were assumed to know the location of the food patch and the nest. This was implemented by means of a food and a nest odour. In nature, foragers can memorise a variety of nest and food source related features that help them locate the nest and the food source (Collett, 2009; Collett et al., 2003). For the purpose of this model, the method of finding the nest and the food source was irrelevant.

#### 2.5. Initialisation

At the beginning of each simulation trial, the nest and the food source were initialised as described above. All agents were initiated at the nest centre; foragers had their state set to idle,

with a probability  $P_{\text{leave}}$  (Table 1) to leave the nest. Receivers performed a random walk after starting each run.

#### 2.6. Submodels

The move-to-nest and move-to-food submodels defined the behaviour of foragers after successful foraging and after leaving the nest, respectively. Agents followed the nest and food odour by sampling 3 patches in walking direction ( $0^\circ$ ,  $45^\circ$  left and  $45^\circ$  right) and moved in the direction of the patch with most odour.

The find-forager submodel defined how receivers in situation III find trophallaxis partners of their own team. Receivers checked at each time step whether their nearest neighbour within the attraction-radius was a returned forager or an unloading forager from the same team. If this was the case, they would move 0.5 patches in the direction of this agent.

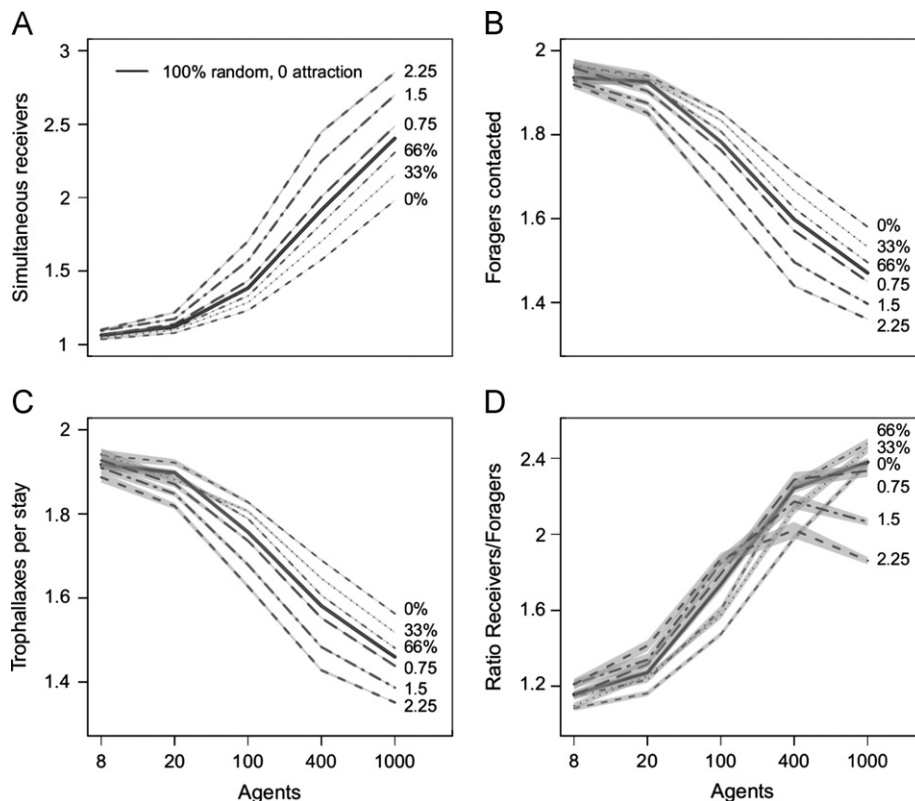
#### 2.7. Sensitivity analysis

In order to test how strongly our results depended on the values of key parameters we tested different values for factors such as the colony size, foraging duration, processing duration, the number of simultaneous receivers or the ratio foragers/receivers. A complete list of values is shown in Table 1.

### 3. Results

#### 3.1. Effect of colony size on delays and information flow

Overall, the time it took a returning forager to find the first transfer partner (unloading delay), the average time it took foragers and receivers to find a transfer partner (average delay) and the time



**Fig. 3.** The effect of non-random interactions on the number of simultaneous transfer partners of foragers, the number of foragers a receiver needed to unload before filling, the number of trophallaxes per hive stay of foragers and the ratio of receivers available for transfer to foragers available for transfer. See legend of Fig. 2 for an explanation of the symbols.

a forager spent in the hive after each foraging trip (hive stay) all decrease with increasing colony size, confirming the findings of an earlier study (Anderson and Ratnieks, 1999) (Fig. 2a–c). However, the model shows that colony size also affects some characteristics of interaction patterns that are of informative value and have not yet been studied. We found that the number of simultaneous receivers is also positively related to colony size (Fig. 3a). Receivers, on the other hand, need to contact fewer foragers until they are full with increasing colony size (Fig. 3b). Equally, foragers engage in fewer transfer contacts until empty with increasing colony size (Fig. 3c). This in turn means that the average transfer durations increase. Colony size also affects the agent balance, i.e. the ratio of receivers available for transfer to foragers available for transfer (Fig. 3d). Overall, there are more receivers available than foragers inside the nest. This is because foragers need time to fly to the food source, and are therefore neither feeding nor in the nest. With increasing colony size, the agent balance changes to become more receiver-biased (Fig. 3d).

### 3.2. Effect of non-random rejection on delays and interaction patterns

The simulation showed that non-random rejection has a strong effect on colony efficiency and interaction patterns. An increasing probability to reject non-team transfer partners by receivers increases the time foragers have to wait until they find an unloading partner (Fig. 2a). The average time increase from complete randomness to complete team-bias ranges from approx. 41% to 54% (Table 2). Also, both the average delay and hive stay duration of foragers increase with an increasing tendency to reject non-team foragers (Fig. 2b,c; Table 2). Non-random interactions lead to an increase in the average delays of approx. 39% to 59%. The total hive stay time increases by approx. 18% to 67% if receivers reject foragers that are not from their team (Fig. 2c; Table 2).

Non-random rejection also affects interaction patterns between foragers and receivers (Fig. 3), but the effect is smaller (Table 2). The number of simultaneous receivers decreases with increasing probability to reject non-team foragers (Fig. 3a).

On the other hand, receivers needed to engage in slightly more frequent transfers before being full if the probability to reject non-team foragers is high (Fig. 3b; Table 2). Foragers also had more transfers (1%–7%) per hive stay if receivers were rejecting non-team members.

**Table 2**

The relative increases and decreases in time delays and worker interactions caused by non-random interactions (100% rejection of non-team foragers; 1.5 patch attraction radius to team members) compared to completely random interactions between foragers (FOR) and receivers (REC) for different colony sizes.

Agents number	8	20	100	400	1000
<i>Non-random rejection vs. random</i>					
Increase in FOR delay	43.7%	52.3%	53.9%	50.7%	40.8%
Increase in Average delay	38.7%	49.2%	50.9%	57.7%	58.6%
Increase in Hive stay	66.6%	57.6%	43.8%	29.1%	17.9%
Decrease in simultaneous REC	2.7%	3.8%	11.1%	17.8%	17.6%
More FOR contacted by REC	1.3%	0.8%	4.0%	6.9%	7.5%
More transfers per hive stay	1.2%	1.2%	4.0%	6.9%	7.1%
<i>Random vs. non-random attraction</i>					
Decrease in FOR delay	29.4%	26.1%	22.1%	9.3%	–3.2%
Decrease in average delay	29.2%	26.6%	25.8%	19.7%	9.1%
Decrease in hive stay	21.8%	22.7%	17.4%	7.9%	1.5%
Increase in simultaneous REC	2.8%	4.6%	13.4%	17.4%	12.2%
Fewer FOR contacted by REC	0.4%	2.7%	4.6%	6.4%	5.0%
Fewer transfers per hive stay	0.4%	2.7%	4.4%	6.2%	5.0%

### 3.3. Effect of non-random attraction on delays and interaction patterns

Non-random interactions caused by non-random attraction affected time delays, hive stay time and interaction patterns (Figs. 2 and 3; Table 2). We found that in most situations, delays and hive stay time decreased due to non-random attraction (Fig. 2; Table 2). Interestingly, the effect on unloading delays was reversed with 1000 agents and foragers had to wait longer in situations with strong non-random attraction (see below for a possible explanation). However, average delays and hive stay duration were always shorter with non-random attraction (average delays: 9%–29%, hive stays: 1.5%–23%; attraction radius of 1.5 patches; Table 2).

Depending on colony size, foragers had approx. 3% to 17% more simultaneous receivers and receivers contacted approx. 0.5% to 6.5% more foragers until full (attraction-radius = 1.5; Table 2). Because foragers had more simultaneous receivers, they required fewer transfers per hive stay to empty (Table 2).

Because strong non-random attraction increases the number of engaged receivers, the ratio of receivers available for transfers to foragers available for transfer decreases when attraction is strong (Fig. 3d). As a consequence, foragers find it harder to find transfer partners and this is likely to explain why foragers have to wait longer until the first transfer if attraction is strong and colonies are large.

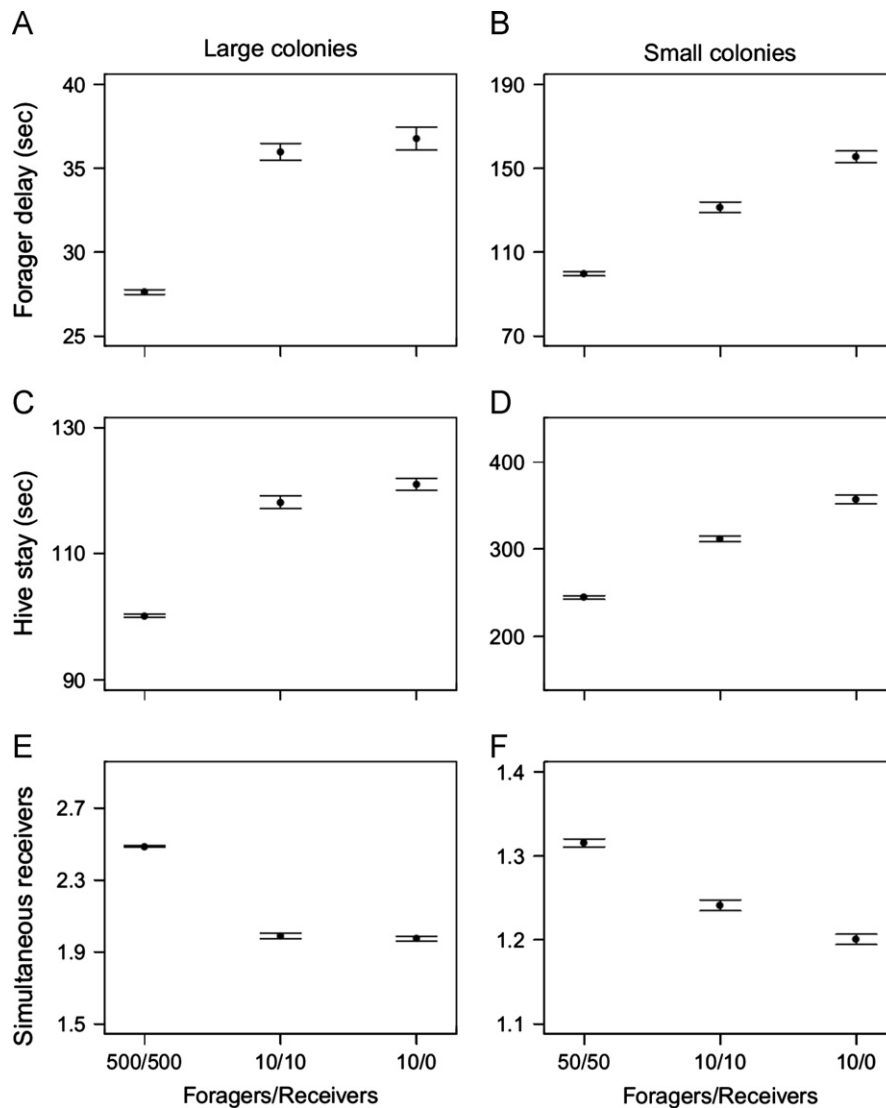
### 3.4. Effect of non-random attraction when one team does not contain receivers

In nature, new types of food such as a new flowering species frequently appear. It has been suggested that foragers that start collecting a new type of food might experience longer unloading delays because there are no or few receivers in the nest that are attracted to this new food type (Farina et al., 2012). Hence, we tested how non-random attraction affects forager delays, hive stay duration and the number of simultaneous receivers experienced by foragers that collect a food type that has no receivers attracted to it, i.e. the team had no receivers.

In large colonies (1000 agents in the large team), the transfer delays of foragers of the teams with few or no receivers (teams 2 and 3) were considerable longer, approx. 25%, compared to team 1 (attraction-radius = 1.0; smaller radii lead to smaller increases) (Fig. 4). Equally, hive stay times increased and the number of simultaneous receivers decreased compared to team 1. In smaller colonies (100 agents in the larger team), the difference between the large and the small teams was reduced if the small team already contained a small number of receivers (Fig. 4).

### 3.5. Effect of agent balance

In nature colonies might often not have even numbers of receivers and foragers and the effect of non-random rejection and attraction might depend on the balance between receivers and foragers (Fig. 5). The simulations showed that the relative effect of non-random interactions indeed strongly depends on the agent balance. If colonies were forager biased (> 70% of foragers) non-random interaction patterns had no effect on the unloading delay, average delay, hive stay time or the number of simultaneous receivers (Fig. 5). The effects of non-random interactions were largest if the two types of agents were more or less balanced (40%–50% foragers). However, in the case of forager unloading delays we found that also in very receiver biased colonies the effect of non-random interactions remained high (Fig. 5A).



**Fig. 4.** The effect of non-random attraction (attraction radius=1.0 patch) on the unloading delay, forager hive stay time and number of simultaneous transfer partners of foragers in colonies with 3 teams, one of which only consists of foragers. The largest team contains either 1000 agents (500 foragers, 500 receivers) or 100 agents (50 foragers, 50 receivers). Two small teams contain 10 foragers each and either 10 or 0 receivers. Mean and standard errors of 10 simulation runs are shown.

### 3.6. The effect of team number

We compared the effect of non-random interactions when there were 1–4 teams in a colony (Fig. 6). Fig. 6a shows that with non-random rejection, unloading delays become even longer with an increasing number of collected food types (i.e. teams). The number of simultaneous receivers is further reduced as team number increases (Fig. 6b). Fig. 6c and d shows that the effect of non-random attraction becomes smaller with more teams. However, the unloading delay was still shorter with 4 teams than when there was no non-random attraction, i.e. interactions were completely random (thick dashed line in Fig. 6c,d).

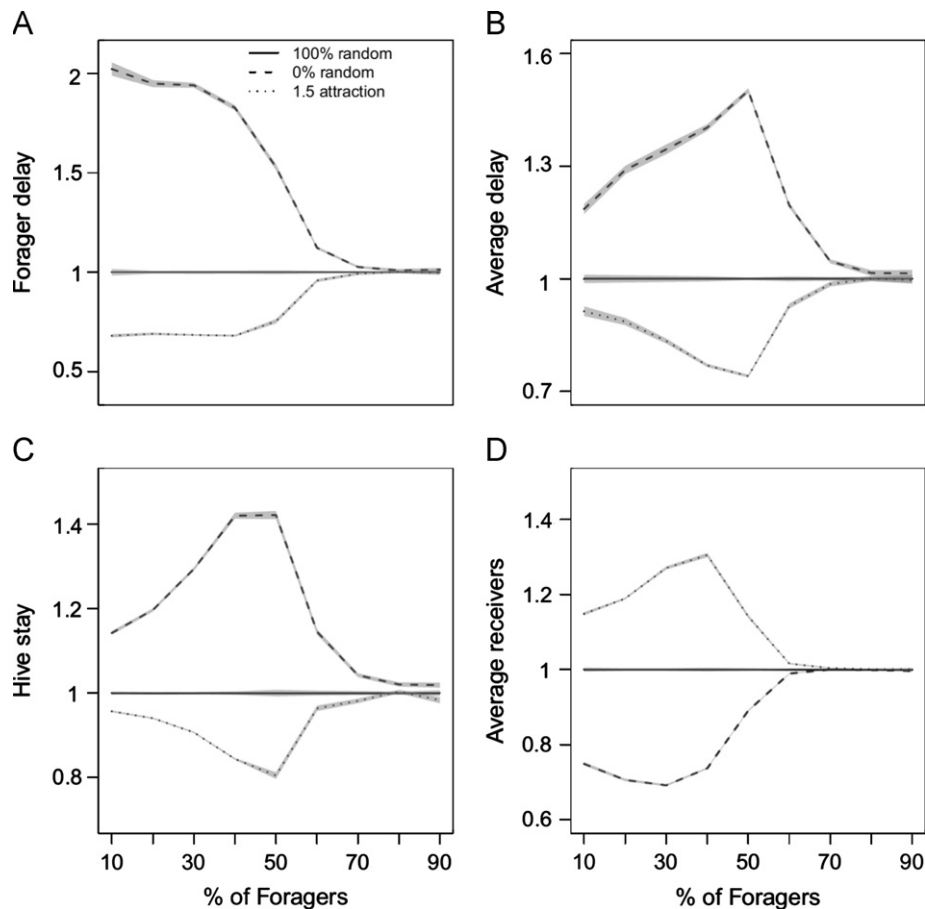
### 3.7. Sensitivity analysis

Many factors were already varied for the simulations presented above. Here we report a few additional manipulations with colonies of 100 agents and present the results for the unloading delays. We found that the effects of non-random interactions were very similar if the foraging and processing durations were doubled. Unloading delays increased by 54% if receivers rejected non-team foragers and decreased by 19.1%

(attraction-radius = 1.5). The effects of non-randomness also do not depend on whether foragers can transfer to multiple or only one receiver. When the receiver number during transfers was restricted to one, non-random rejection increased the unloading delay by 60%, while non-random attraction decreased it by 27.3 (attraction-radius = 1.5).

## 4. Discussion

The results of our study show that non-random interactions in task-partitioning with direct transfers affect colony efficiency measured as the time delays experienced by foragers and receivers searching for a transfer partner and the total hive stay time of foragers. If receivers reject foragers, time delays experienced by foragers and average delays of foragers and receivers increase by approx. 39%–59% (Table 2). Foragers also need slightly more transfers to completely unload their crop. As a consequence, total hive stay time of foragers increases too (18% to 67%). The effect of non-random rejection on hive stay times of foragers is particularly large in small colonies. Non-random rejections also decreased the number of simultaneous receivers. On the other hand, since foragers



**Fig. 5.** The effect of non-random interactions on unloading delays (A), average delays (B), hive stay time (C) and the number of simultaneous transfer partners of foragers (D) depending on the agent ratio. The colony size was always 100 agents; agents were divided into two equally sized teams. The x-axis shows the number (and percentage) of foragers in the colony; the y-axis shows the relative effect of non-random rejection (dashed line) and non-random attraction (dotted line) when compared to random interactions.

and receivers require slightly more contacts per foraging and processing cycle, the acquisition of information about unloading delays might be improved. Multiple transfers can improve the accuracy of information about time delays, potentially leading to a more accurate response to the experienced transfer delays (Ratnieks and Anderson, 1999b). On the receiver side, more transfers could improve olfactory learning because more learning trials improve memory acquisition (Menzel, 1999). For most simulations we assumed that only 2 different types of food were collected (2 teams). If the number of food types increases, rejecting foragers offering the wrong type causes even further increases of time delays because the pool of potential transfer partners becomes smaller.

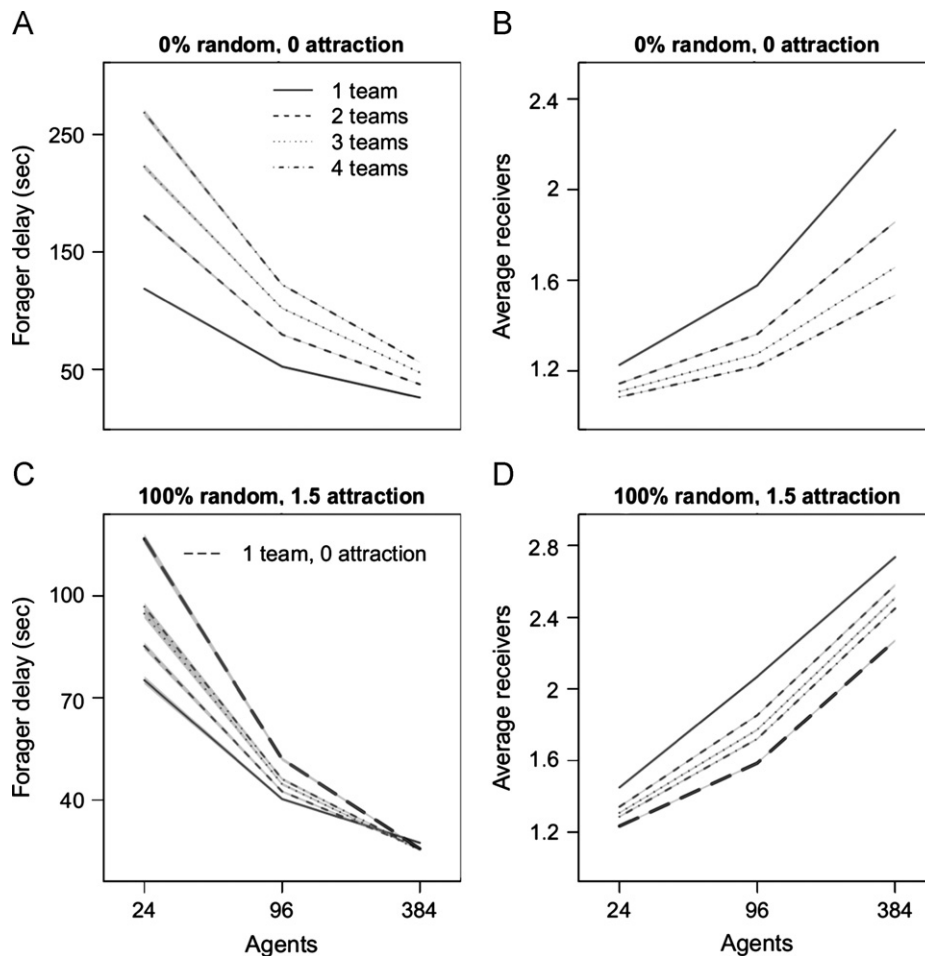
Given the negative ergonomic consequences of non-random rejection, is it likely to occur in nature? Martinez and Farina (2008) found that the sucrose-concentration of liquid food transferred by a honey bee forager correlated positively with the sucrose-response threshold of the receiver. This indicates that receivers might accept nectar that is above their sugar concentration acceptance threshold, while rejecting foragers offering nectar below this threshold. Also leaf-cutter ants learn to avoid certain types of leaves based on odours and texture (North et al., 1999; Saverschek and Roces, 2011). Since leaf-cutting foragers sometimes directly transfer leaf-fragments (Hubbell et al., 1980), non-random rejection can potentially occur. In this case, however, non-random rejection is beneficial because it prevents colonies from collecting food that is damaging for their fungus garden.

Non-random attraction improved colony efficiency by decreasing the unloading delay and average delays by up to 29% (attraction-radius: 1.5; Table 2). Smaller attraction radii lead to smaller gains.

Non-random attraction also decreased forager hive stay time and increased the number of simultaneous receivers. On the other hand, foragers and receivers in our study had slightly fewer (but longer) transfers per foraging and processing cycle, which could reduce opportunities to acquire information (Ratnieks and Anderson, 1999b). The effect of attraction was largest if all agents belonged to the same team (Fig. 6c,d). That is, from an ergonomic perspective colonies would do best if all foragers would collect the same food type. An increasing number of food types reduce the positive effects of non-random attraction.

We argue that non-randomness caused by attraction is potentially widespread in nature, particularly when transferring liquid food. Our findings suggest that mechanisms which improve the ability of receivers (or donors) to recognise potential transfer partners are highly beneficial because they decrease waiting delays, which are a major cost of task-partitioning (Ratnieks and Anderson, 1999a). Appetitive olfactory learning is widespread in social insects (honey bees: (von Frisch, 1919); ants: (Roces, 1990); bumblebees: (Laloi et al., 1999); wasps: (McPheron and Mills, 2007); stingless bees: (Mc Cabe et al., 2007)) and provides a simple mechanism to cause such non-random attraction. Non-random interaction can potentially also occur when workers transfer solid materials. Ant workers acquire preferences for solid materials such as types of leaf-fragments (Roces, 1990, 1994) or seeds (Rissing, 1981), and both kinds of food can be directly transferred from worker to worker during foraging (Ratnieks and Anderson, 1999a) (Even though leaf and grass fragments are mostly transferred indirectly, worker-worker interactions on the trail can potentially lead to information transfer (Bollazzi and Roces, 2011)).





**Fig. 6.** The effect of team number (1–4) on unloading delays and the number of simultaneous transfer partners of foragers in colonies of different sizes. (A) and (B) show a situation where the probability of receivers to accept non-team foragers is 0%. With one team (solid line), 0% and 100% randomness yield the same results because there are no non-team agents. (C) and (D) show a situation where interactions are 100% random and receivers are attracted to foragers of their own team (attraction-radius = 1.5). The thicker line shows a situation with one team, no attraction and 100% randomness (control).

Non-random interactions might potentially also affect foraging effort. In honey bees, for example, both the unloading delay (Lindauer, 1948; Seeley et al., 1991; Seeley, 1989; Seeley and Tovey, 1994; Lindauer, 1954) and the number of receivers (Farina, 2000; De Marco, 2006; Grüter and Farina, 2009) affect the probability of foragers to perform recruitment dances, suggesting that non-random rejections could potentially reduce overall recruitment and foraging activity, whereas non-random attractions would have positive effects on recruitment intensity of foraging effort. Accordingly, Grüter and Farina (2009) found that foragers returning with food types familiar to receivers had more transfer partners than foragers returning with unscented food or food with a novel odour and they were followed by more bees when performing recruitment dances.

However, our simulations suggest that non-random attraction due to learning of collected material could also have negative consequences for the foraging success of a colony if a new and superior food type appears. A forager returning with a novel food type is likely to experience longer unloading delays and fewer transfer partners, which in turn will cause less recruitment dances (Farina et al., 2012). We simulated this by having colonies with a small group of foragers, but with either no corresponding group of receivers or only a small group of receivers attracted to these foragers (Fig. 4). The unloading delays and hive stay times of foragers collecting this “novel” type of food increased considerably compared to the other foragers of the same colony and they

had fewer simultaneous receivers. This could mean that non-random attraction makes honey bee colonies slower in switching to new food types if the environment changes. On the other hand, foragers returning with a new, highly profitable food source might search for receivers more vigorously (e.g. by walking faster and contacting more receivers) and, thereby, compensate for the lack of interest shown by receivers. These predictions should be tested experimentally.

Our simulations suggest that the effects of non-random interactions depend on the balance between receivers and foragers, with more even ratios leading to larger effects (Fig. 5). The ratio of receivers to foragers is likely to be very variable, even during a day, but colonies of many insect species might have means to maintain an optimal balance. In nectar foraging honey bees and nest-building paper wasps, the length of transfer delays experienced by one worker group allows these workers to adjust their behaviour in ways that help maintain an optimal balance between the different groups (honey bees: reviewed in Anderson and Ratnieks (1999); wasps: (Jeanne, 1986)). This agent balance can potentially also affect colony foraging patterns: a recent theoretical study found that the agent-balance affects forager allocation to food sources in a changing environment (Schmickl et al., 2012).

So far, little attention has been paid to non-randomness in worker–worker interactions and, therefore, empirical evidence for non-random interactions is scarce (e.g. Goyret and Farina, 2005).

Given the ergonomic implications of non-randomness further research is needed to explore how common biases during worker–worker interactions are.

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## Appendix A. Supplementary materials

Supplementary materials associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2013.02.013>.

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