How to not get stuck—Negative feedback due to crowding maintains flexibility in ant foraging

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HIGHLIGHTS

- Ants employ pheromone trails and positive feedback to choose the best food source.
- Positive feedback allows rapid decisions, but causes ants to be trapped in local optima.
- Recent empirical studies discovered two negative feedback processes in ant foraging.
- Using an agent based model, the roles of these two processes are tested.
- Negative feedback due to crowding is found to save colonies from becoming trapped.

ARTICLE INFO

ABSTRACT

Ant foraging is an important model system in the study of adaptive complex systems. Many ants use trail pheromones to recruit nestmates to resources. Differential recruitment depending on resource quality coupled with positive feedback allows ant colonies to make rapid and accurate collective decisions about how best to allocate their work-force. However, ant colonies can become trapped in sub-optimal foraging decisions if recruitment to a poor resource becomes too strong before a better resource is discovered. Genetic algorithms and Ant Colony Optimisation heuristics can also suffer from being trapped in such local optima. Recently, two negative feedback effects were described, in which an increase in crowding (crowding negative feedback—CNF) or trail pheromones (pheromone negative feedback—PNF) caused a decrease in subsequent pheromone deposition. Using agent based simulations with realistic parameters I test whether these negative feedback effects can prevent simulated ant colonies from becoming trapped in sub-optimal foraging decisions. Colonies are presented with two food sources of different qualities, and these qualities switch part way through the experiment. When either no negative feedback effects are implemented or only PNF is implemented colonies are completely unable to refocus their foraging effort to the high quality feeder. However, when CNF alone is implemented at a realistic level 97% of colonies successfully refocus their foraging effort. This ability to refocus colony foraging efforts is due to the strong reduction of pheromone deposition caused by CNF. This suggests that CNF is an important behaviour enabling ant colonies to maintain foraging flexibility. However, CNF comes at a slight cost to colonies when making their initial foraging decision.

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1. Introduction

The organisation of social insects is an important example in collective organisation and distributed decision making (Bonabeau et al., 2000). Honey bee swarming and ant recruitment have been the inspiration for swarm intelligence and algorithms based on ant colony optimisation (Bonabeau et al., 1999; Dorigo and Stützle, 2004). Such

collective decision making systems are capable of producing near-optimal solutions to np-hard problems–problems where the optimal solution can only be found by trying all possible solutions (Dorigo and Stützle, 2004). Traditional exact algorithms based on mathematical equations cannot be used to find solutions to such problems. Social insect inspired algorithms are based on two linked concepts: communication and positive feedback.

While the foraging systems of real ants vary greatly amongst species, ant-based algorithms are usually modelled on a foraging method termed mass recruitment (Hölldobler and Wilson, 1990), which requires no direct interaction between

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individuals. A generalised bout of such foraging begins with multiple scouting ants exploring the environment, until a resource is located. When a scout locates a resource it returns to the nest, depositing a pheromone trail (Wilson, 1962), the strength of which is modulated according to many factors, including the quality of the resource (Beckers et al., 1993; Hangartner, 1970; Verhaeghe, 1982). Ants in the nest sense the pheromone trail, exit the nest, and follow the pheromone trail to the food source. The number of ants exiting the nest is a function of the strength of the pheromone (Hölldobler et al., 1978; Wilson, 1962). Thus, as more ants locate the resource and return to the nest depositing pheromone, more ants are recruited from the nest–a positive feedback cycle. When presented with two pheromone trails, ants follow the trails in a manner relative to the relative strengths of the trails (Hangartner, 1969; Verhaeghe, 1982). If two identical food sources are discovered simultaneously, small initial differences in pheromone trail strengths will be amplified by positive feedback, resulting in the colony concentrating foraging effort on one of the food sources—a phenomenon termed symmetry breaking (Beckers et al., 1990; De Biseau et al., 1991; Grüter et al., 2012; Sumpter and Beekman, 2003). Such symmetry breaking also occurs when colonies are offered two identical routes to a single food source (Beckers et al., 1992a; Deneubourg et al., 1990; Goss et al., 1989). This amplification of small differences in initial pheromone concentrations, combined with ants depositing more pheromone to higher quality resources, allows ant colonies to focus their foraging efforts on the better of two simultaneously discovered food sources (Beckers et al., 1990). Positive feedback is also the driving mechanism behind collective decision making during honey bee swarming, when a new nest site must be selected (Seeley and Buhrman, 2001). Such positive feedback systems allow colonies to make rapid collective decisions, without any one individual comparing all possible options.

However, such positive feedback seems to come at the cost of flexibility. In a classic study, Beckers et al. (1990) demonstrated that when the mass recruiting ant *Lasius niger* is presented initially with a low quality food source, and only later given access to a higher quality food source, the colony is unable to switch its collective foraging effort to the higher quality food source. This is because the pheromone trail leading to the poor food source has become so strong that new trails leading to the better food source are not strong enough to 'compete' for followers with the well-established trail. This has also been demonstrated in abstracted models of ant foraging (Camazine et al., 2003; Goss et al., 1989; Nicolis and Deneubourg, 1999; Sumpter and Beekman, 2003). Ants which do not use such mass recruitment do not suffer from these problems and can dynamically follow changing resource qualities (Dussutour and Nicolis, 2013). Such inflexibility seems maladaptive, and its presence is thus puzzling. Indeed, in the field ant colonies can be seen to forage simultaneously on multiple food sources (Devigne and Detrain, 2005; Dreisig, 1988). This may in part be explained by the limited nature of natural resources: when laboratory ant colonies were provided with feeders capable of supporting only a limited number of foragers, colonies were able to refocus their foraging effort from a lower-rate feeder to a higher-rate feeder (Grüter et al., 2012). However, Latty and Beekman (2013) report that the mass-recruiting ant *Pheidole megacephala* is capable of dynamic switching between non-rate limited artificial food sources of different qualities when these qualities are switched. One potential mechanism for enabling such flexibility would be active cross-inhibition, with ants recruiting to a newly discovered food source actively inhibiting recruitment to other food sources, as occurs during house-hunting in honey bees (Seeley et al., 2011). However, such behaviour has not to our knowledge been reported in ants. A second possible mechanism, proposed by Reid et al. (2013), would be to disproportionately

strengthen incipient trails, perhaps by ants performing U-turns to re-mark new trails. Another potential but untested mechanism for strengthening incipient trails would be by employing two attractive pheromones, only one of which is deposited during initial recruitment (Dussutour et al., 2009b). Private information held by the forager, such as the location of an alternative food source or compass information, which can be used to over-ride social (pheromone) information, perhaps coupled with some noise during pheromone following, could also in principle allow foraging flexibility (Dussutour et al., 2009a; Ramsch et al., 2012). Another potential way of maintaining such foraging flexibility would be by weakening established trails, or preventing them from becoming too strong. This could be achieved by the implementation of negative-feedback mechanisms to counteract the positive feedback recruitment cycle, and thus to prevent trails from becoming too strong. Somewhat similar to this may be the addition of stochasticity to the ant's trail following abilities, allowing ants to discover food sources more easily, being more likely to follow the weaker of multiple trails, and weakening the 'trapping' effect of pheromone trails (Deneubourg et al., 1983). Small differences between the amount of pheromone deposited for good versus poor feeders may also allow colonies to maintain foraging flexibility (De Biseau et al., 1991). Lastly, ants which can also use individual-based recruitment (e.g. tandem running) may be able to use break out of pheromone-trail induced trapping (Beckers et al., 1990).

Recently, two such negative feedback effects have been described in the ant *L. niger* (Czaczkes et al., 2013a, 2013b), responding to pheromone levels and crowding levels on the trail respectively. In the pheromone negative feedback effect (PNF) ants were seen to reduce pheromone deposition when walking on trails already heavily marked with trail pheromone (Beckers et al., 1992b; Czaczkes et al., 2013a). In the crowding negative feedback effect (CNF) ants were seen to reduce pheromone deposition in response to head-on encounters with other foragers on the trail (Czaczkes et al., 2013b), independent of PNF. Both of these negative feedback effects should result in limiting the strength of well-established pheromone trails, perhaps setting an upper limit to their strength. This may, in turn, allow ant colonies to maintain flexibility. Furthermore, such negative feedback effects should not affect colonies in the early stages of recruitment as the levels of crowding or strength of pheromone trails are low, and so should not affect the speed or accuracy with which an initial collective decision is made. Only the ability to refocus foraging effort should be affected.

The effects of these negative feedback effects on collective foraging decisions have yet to be examined. As it is not possible to prevent real ants performing these negative feedback behaviours *in vivo*, I have taken an *in silico* modelling approach to testing these hypotheses. An effect similar to PNF was included by Bandeira de Melo and Araújo (2011) along with many other behavioural rules in an ant foraging model which showed the ability to overcome stagnation, but its role was not explicitly considered. Using agent based models with realistic parameters I model a generalised ant foraging system in which I implement the PNF and CNF effects. Spatially and temporally explicit agent-based models are well suited to investigating emergent spatial systems such as ant trail networks (Fahse et al., 1998), and have been used successfully to model many aspects of social insect organisation (Grüter et al., 2013; Jackson et al., 2011; Robinson et al., 2008). Here, colonies are presented with two food sources of different qualities, and these qualities are switched part way through the experiment. At realistic levels PNF does not have an impact on colony level flexibility. However, CNF has a large effect on colony level flexibility, allowing colonies to adaptively track changes in the quality of food sources. CNF did, however, come at a slight cost to

colonies when making their initial foraging decision, before the feeder qualities were switched.

2. Methods

I developed a spatially explicitly agent based model using the modelling program Netlogo 5.0.3 (Wilensky, 1999). The Netlogo file, including the annotated program code, is provided as an online supplementary material (OSM 1), and can be run using the Netlogo program which is freely available at http://ccl.northwestern.edu/netlogo/. A plain text file of the code is also provided. The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2010, 2006).

2.1. Overview

2.1.1. Purpose

The purpose of the model was to explore the effects of two negative feedback effects described in the *L. niger* foraging system, namely contact with other ants and presence of trail pheromone causing foragers to deposit less trail pheromone (Beckers et al., 1992b; Czaczkes et al., 2013a, 2013b). While the model is parameterised, where possible, from empirical studies, it is not designed

to be an exact model of *L. niger,* but instead to capture the salient elements of foraging organisation.

2.1.2. Entities, state variables, and scales

The model is spatially explicit, consisting of a grid of 300 by 200 patches (the environment) and populated by agents (the ants). The model is temporally explicit, with 1 time-step being equivalent to 1 s. The model runs for 5000 time-steps (≈ 83.3 min). Global variables, which can affect the agents or the patches, are also modelled. A list of parameters for agents, patches, and global variables, is provided in Table 1.

2.1.3. Process overview and scheduling

The environment is formed by defining one patch at coordinates 0, -80 as the nest, and patches in a 4 patch radius centred on coordinates 130, 80 and -130, 80 as the right and left food patches, respectively. The food patches are thus circa 150 patches away from the nest entrance. As *L. niger* workers walk at circa 3 cm per second (Czaczkes et al., 2011), the distance between the feeders and the nest corresponds to approximately 450 cm. The left and right food sources have a quality set at 50 and 100, respectively. A quality of 50 corresponds to a one molar sucrose solution. One agent is spawned at the centre of each food patch to simulate simultaneous discovery of the two patches, and thereafter one agent is spawned,

Table 1
Agent, patch, and global variables.

Variable	Values	Description
Agents		
X and *Y* coordinates	*X* coordinate: -150–150 *Y* coordinate: -100–100 Non-integer	Every agent has an explicit location on the grid
State	"Scouting" or "returning"	Ants may be either searching for food by random search or by following pheromone trails, or may be returning from a food source to the nest
Memory	"Yes" or "no"	Ants may have been to a food source before ("yes") or not ("no"). This affects the behaviour of "scouting" ants, allowing them to "know" that they must follow pheromone trails away from the nest, as real ants do
Lastfood	"None", "left" or "right"	The last food source the ant has visited–this tells the model to which tally to assign the food the ant returns
Crowding	Number, an integer, 1	A measure of crowding experienced. 1 point is added for every other agent the agent shares a patch with every time-step. This value is reset on reaching the nest, modelling rapid response to a changing crowding environment (Czaczkes et al., 2014)
Patches		
X and *Y* coordinates	*X* coordinate: -150–150 *Y* coordinate: -100–100 Integer	Every patch has an explicit location. Patches cannot move
Pheromone	Number, non-integer, 0	The amount of trail pheromone on the patch
Patchtype	"Nothing", "food1", "food2", or "nest".	This defines whether the patch is empty environment ("nothing"), a food patch ("food1" or "food2") or the nest entrance ("nest")
Global variables		
Pheromone diffusion rate	Number, non-integer, 0–1. Modelled as 0.02	The rate at which pheromone diffuses from one patch into the 8 neighbouring patches. A proportion equal to this number is removed from the patch every time-step and distributed equally to the 8 neighbouring patches
Pheromone-negative-feedback (PNF)	Number, an integer, 0. levels modelled: 0, 25, 50, 75, 100	How strong an effect patch pheromone levels have on agent pheromone deposition. 0=no effect. 50=realistic effect level based on empirical data from Czaczkes et al. (2013a)
Crowding-negative-feedback (CNF)	Number, an integer, 0. Levels modelled: 0, 25, 50, 75, 100	How strong an effect an agent's crowding variable has on the agents' pheromone deposition. 0=no effect. 50=realistic effect level based on empirical data from Czaczkes et al. (2013b)
Right and left food quality	Number, an integer, 0. Levels modelled: 50, 100	The quality of the two food patches. 50 corresponds to a 1 M sucrose solution in terms of how strong a pheromone trail a returning ant deposits
Extra ants right and left	Number, an integer, 0 Modelled as 1 and 1	The number of agents spawned at each food source at the start of each trial. This allows simultaneous discovery of both feeders
Min-pheromone-differentiation	Number, non-integer, 0 Modelled as 0.198	The level of pheromone on a patch below which ants react as if there is no pheromone on the patch. Modelled so that pheromone deposited by an ant returning from a food source with quality=50 (=1 mol sucrose solution) becomes undetectable in 2700 time-steps (=45 min, 1 time-step=1 s). Based on empirical data from Beckers et al. (1993)
St-dev	Number, non-integer, 0 Modelled as 30	Affects how sinuous the paths of scouting and returning ants are. A number is randomly chosen from a normal distribution with a mean of 0 and a standard deviation of "St-Dev".
Colony size	Number, non-integer, 0 Modelled as 250	The number of active foragers
Time-to-switch	Number, non-integer, 0. set at 1200	The number of time-steps before the starting qualities of the left and right food patches switch. 1200 time-steps ≈ 20 min

facing a random direction, from the nest every time-step until the total number of agents reaches the colony size (set at 250). Agents begin in the state "scouting", and travel using a correlated random walk around the environment. In later stages of the simulation scouting ants also follow pheromone trails, with ants that have been to a food source before travelling away from the nest, as is the case with real ants (Czaczkes and Ratnieks, 2012). On reaching a food source ants take the state "returning", turn around and begin walking in the direction of the nest, depositing a pheromone trail with a strength dependent on the quality of the food source they last visited ($F_{quality}$), the amount of crowding the ant experienced, the amount of pheromone already on the patch the ant is occupying (P_{patch}), and the strength of both negative feedback effects (CNF and PNF). On reaching the nest the quality of the food source the ant visited is added to a running tally of food returned, the ant turns around and returns to the "scouting" state. After a set number of time-steps (set at 1200, ≈ 20 min) the quality of the two food sources switches, with right taking the quality 50 and left the quality 100. An annotated screenshot of the model is provided in Fig. 1.

During the simulation the behavioural states and variables of each agent and patch are updated asynchronously, in the order: ants count other ants on patch→ants check state→ants walk→ants check crowding level and pheromone level on current patch and lay pheromone accordingly→trail pheromone diffuses→global measurements taken. See the fully commented code provided in OSM 1 for details.

2.1.4. Design concepts

The model uses the basic principle of pheromone deposition and following by ants resulting in adaptive colony-level decisions. By depositing more pheromone to better quality food sources, and preferentially following stronger pheromone trails, ant colonies can focus their foraging on the better food source (Beckers et al., 1992b, 1990; Grüter et al., 2012; Hangartner, 1970, 1969). This, however, may come at the cost of flexibility; the colony may not be able to adaptively switch its efforts in response to environmental changes (Beckers et al., 1990; Grüter et al., 2012; Sumpter and Beekman, 2003).

The proportion of agents exploiting the two food sources is an emergent property of the system, as well as the possible ability for the proportion of agents exploiting the two food sources to track changes in the food source quality. Lastly, the total amount of food

returned to the colony over the course of the experiment emerges from the behaviour of individual agents.

Agents are capable of following pheromone trails and of depositing pheromone trails relative to the food quality ($F_{quality}$), and to pheromone levels on their patch (P_{patch}), or crowding levels sensed if these abilities are activated. Thus, agents can sense the number of other agents on their current patch, and the level of pheromone on their current patch. Agents returning to the nest are assumed to know the location of the nest. Agents interact with each other only via causing an increase in each-others' crowding counter, and indirectly by depositing pheromone. Stochasticity is used to introduce variation into the paths of the ants, both during scouting and when returning to the nest. This allows agents to explore the environment and discover the food sources or pheromone trails. Although other real world ant behaviours are also subject to variation, I chose to keep this variation to a minimum, so as to increase the repeatability of the models. Observations are taken at time-step 1200 (the time at which the food qualities switch) and at time-step 5000 (when the model ends), and include the number of ants currently returning from either food source as a measure of which food source is being preferentially exploited, the total amount of food retrieved, and the total amount of pheromone present in the world.

Agents have no explicit objectives, do not learn, and do not attempt to predict the future state of the model. There are no intermediate levels of organisation, such as groups or collectives, in the model.

2.1.5. Details

At the beginning of the model the environment was set up as above and as detailed in OSM 1. Pheromone levels on all patches begin at 0. No other external sources of data were used.

Pheromone deposition is modelled as follows:

When both pheromone-negative-feedback and crowding-negative-feedback effect strengths=0, returning ants deposit an amount of trail pheromone equal to the quality of the feeder they are returning from every time-step.

When both CNF and PNF are activated, the effects are cumulative: first the amount of pheromone to be deposited if only CNF was active is calculated, and then the PNF calculation is performed on this value, as follows:

$$E_{cnf} = \frac{F_{quality}}{(CNF \times 0.004 \times crowding + 1)}$$

$$P_{deposit} = \frac{E_{cnf}}{(PNF \times 0.0000286 \times P_{patch} + 1)} \quad (1)$$

every time-step, where $P_{deposit}$ is the amount of pheromone to be deposited on the patch the agent is on, $F_{quality}$ is the most recent food source quality the agent experienced, CNF is the crowding negative feedback effect strength, PNF is the pheromone negative feedback effect strength, and P_{patch} is the pheromone level already on the patch before pheromone deposition. The constant of 0.0000286 was chosen so that an ant walking on a trail on which 28 ants have deposited pheromone from a 1 M sucrose feeder will deposit 1/3 of the pheromone they would have deposited if no pheromone was present on the trail when pheromone-negative-feedback effect strength=50. This value was taken from empirical data collected in Czaczkes et al. (2013a). In that experiment 4 ants made 7 return journeys to a 1 M sucrose food source, and the effect of the trail pheromone they laid reduced pheromone deposition to a third of the amount of pheromone deposited by ants for whom pheromone on the trail was removed (see Fig. 6B in Czaczkes et al., 2013a). Values 0, 25, 50, 75, and 100 for the *pheromone-negative-feedback effect strength* were tested. The constant of 0.004 was chosen so that an ant that experienced 10 ants
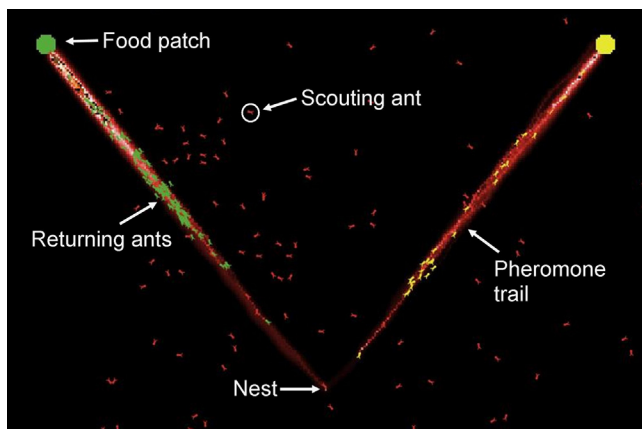

Fig. 1. Annotated screenshot from the model during a simulation run. Red ants are scouting or following a pheromone trail. Yellow and green ants are returning from the right or left food source, respectively. The brightness of the pheromone trail is proportional to its' strength. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
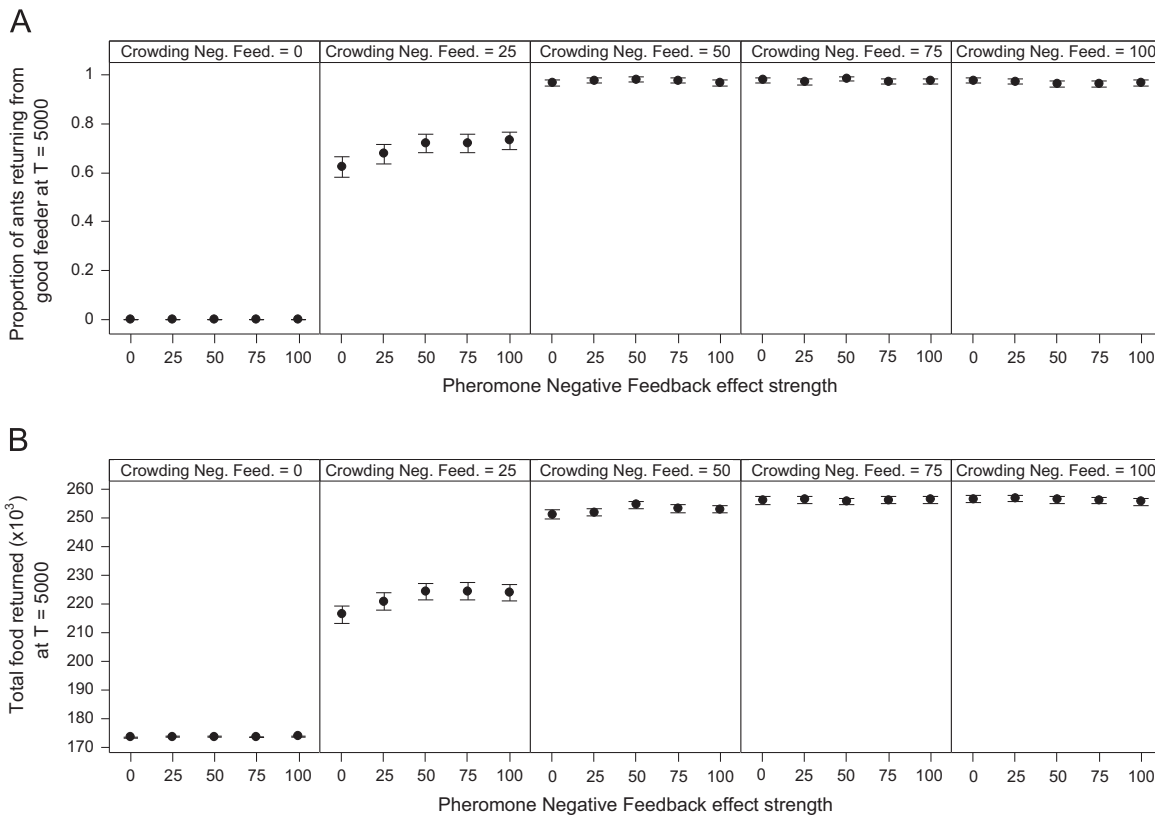
Fig. 2. Proportion of ants returning from the superior of two food sources (A) and total food returned (B) to the simulated ant colony at the end of the trial (time-step 5000), at different strengths of pheromone negative feedback and crowding negative feedback effects. A value of 50 represents the realistic effect strength, as parameterized from empirical research. Dots are means, whiskers at 95% confidence intervals for the mean. Each permutation was run 500 times.
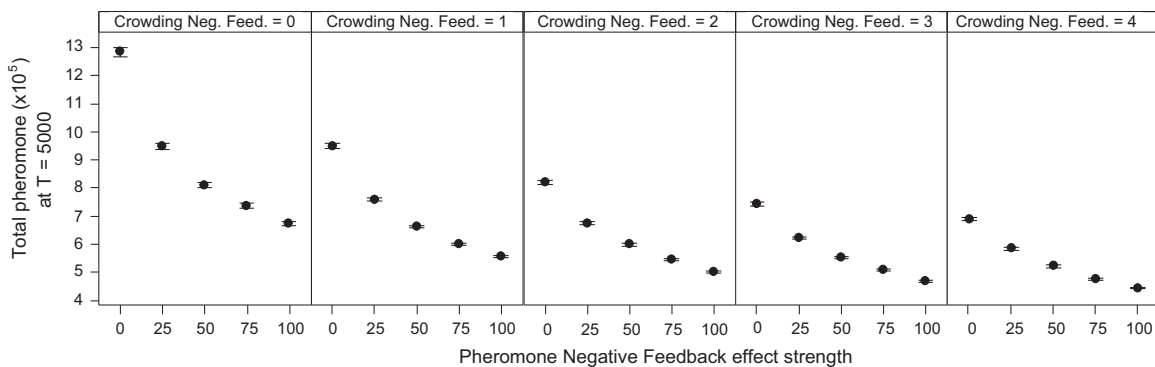
Fig. 3. The total pheromone present in the world at the end of a trial (time-step=5000) at low crowding negative feedback effect strength. Note that the CNF levels in this figure are very low (0–4), not the levels in the figures above. Dots are means, whiskers at 95% confidence intervals for the mean. Both effects reduce pheromone levels, and have their main effect at very low levels, but CNF has a much stronger effect than PNF. Dots are means. Horizontal lines represent upper and lower 95% confidence intervals, but are too close together to be discerned.

when *crowding-negative-feedback effect strength*=50 deposits 30% of what it would deposit if it experienced no crowding. This is based on empirical data from Czaczkes et al. (2013b). In that experiment individual ants encountering 10 glass beads treated to mimic nestmate ants reduced their pheromone deposition by 30% as compared to ants which encountered untreated control breads (see Fig. 3 in Czaczkes et al., 2013b). Crowding values are reset to 1 when an ant reaches the nest, approximating the behaviour of real ants experiencing changes in crowding levels (Czaczkes et al., 2014). Values 0, 25, 50, 75, and 100 for the *crowding-negative-feedback effect strength* were tested.

The pheromone deposition function is visualised in OSM 2. Every combination of CNF and PNF was simulated 500 times. As

the relative effect of CNF on total pheromone deposition becomes weaker at higher value levels (see results), I also ran simulations with CNF at a very low level (1, 2, 3 and 4) to explore the effect of CNF at low levels on pheromone deposition.

Pheromone on a patch decays by diffusing onto the 8 neighbouring patches. Every time-step 2% of the pheromone on a patch is distributed amongst its 8 neighbours. This means a standard pheromone deposition of 50 decays to circa 0.198 in 2700 time-steps, or circa 45 min. The pheromone detection threshold of the ants was set to 0.198. Beckers et al. (1993) estimated that a single pheromone deposition of *L. niger* to become undetectable in circa 45 min. Pheromone decay was modelled as a diffusion process to produce wide pheromone paths with a strength gradient from the

centre outwards, allowing ants to turn towards area of high pheromone and thus follow the path, mimicking real pheromonal navigation (Hölldobler and Wilson, 1990).

The correlated random walk of scouting ants is implemented by having each agent draw a random number from a Gaussian distribution with a mean of 0 and a standard deviation of 30 (see OSM 3 for a sensitivity analysis of this value). The agent then turns right by that number of degrees (note that half of the numbers drawn will be negative), and moves forward one patch width.

Trail following behaviour is implemented by having each agent measure and compare the pheromone level of the patch ahead of it, ahead and to the right, and ahead and to the left. The ant then turns towards the patch with the highest pheromone and moves forward one patch width. Pheromone level differences below the perception threshold of the agents are ignored. The threshold was set so that a single deposition from a standard strength (50) food source, with no negative feedback effects, would decay in c. 2700 time-steps, the equivalent of 45 min. This value was based on pheromone decay rates of *L. niger* calculated by Beckers et al. (1993).

Details of all sub-models can be found in OSM 1.

Due to the large number of replicates per permutation (500) statistical tests are not necessary, and conclusions can be drawn directly from the figures (White et al., 2014).

2.1.6. Sensitivity analysis

There are several variables and parameters in the model which, while not being directly relevant to testing my hypotheses, may have influenced the results of the model. Such variables include the world size, number of foragers, the delay until the quality of the feeders are switched, the presence of initial discovering ants, the location (left or right) of the initially high quality food source,

the rate at which the pheromone diffused, the variability of the ant's correlated random walk, the relationship between food quality and pheromone deposition, and the order in which procedures were carried out in the model. These were systematically varied, and their effect on the collective behaviour of the ant colonies examined (see OSM 3).

3. Results

My main hypothesis regarding the negative feedback effects was that they would allow colonies to maintain flexibility in a changing environment, allowing colonies to refocus their foraging efforts on the best food source after a change, thus resulting in an increase in food returned to the nest. Crowding negative feedback (CNF) had a strong positive effect on the proportion of ants returning from the superior food source by the end of the model run, which is a measure of how effectively the colony switched from exploiting one food source to exploiting another. This is reflected in increased total food retrieval. By contrast, increasing PNF strength had little effect on the ability of colonies to refocus their foraging efforts, and consequently had little effect on food retrieval (Fig. 2A and B).

I also examined the effect of the negative feedback effects on total pheromone present in the model at the end of each trial. As expected, both negative feedback effects had a strong effect on total pheromone present; stronger negative feedback effects resulted in less pheromone being deposited. The reduction in total pheromone deposition is very strong even for very low levels of CNF (see Fig. 3). The effect of CNF was much greater than that of PNF. The two effects also interact: As the one effect becomes stronger, the effect of the other on pheromone deposition became weaker.
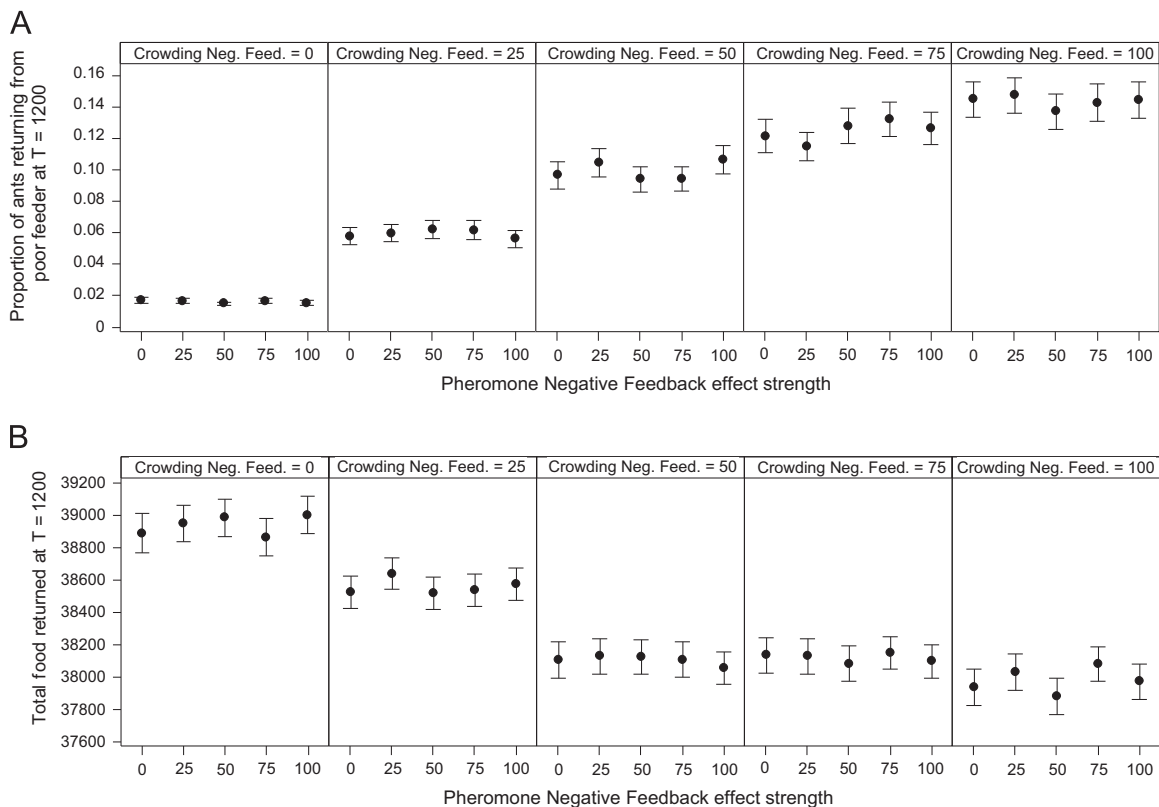
Fig. 4. Proportion of ants returning from the food sources at the time when the food sources switch quality (time-step=1200), at different crowding negative feedback (CNF) effect strengths. Stronger CNF result in a smaller proportion of ants returning from the superior feeder, demonstrating a less cohesive decision.

My second hypothesis was that the increase in flexibility engendered by the negative feedback effects would not have a detrimental effect on how rapidly or accurately colonies can make an initial collective decision. I explored this possibility by considering the behaviour of colonies at time-step 1200—the exact point in which the quality of the feeders was switched. PNF indeed had no effect on the proportion of ants returning from the poor quality feeder or the total food intake at time-step 1200 (see Fig. 4A and B). However, contrary to my prediction, CNF did negatively affect colony level performance before the food quality switch (see Fig. 4A and B). Higher CNF levels resulted in a higher proportion of ants returning from the low quality feeder. The colony level decision was less cohesive at higher CNF levels. This in turn resulted in a lower total food intake up to the point of feeder quality change.

The results of the sensitivity analysis demonstrated that the general pattern of CNF improving the ability of ant colonies to refocus their foraging efforts is robust to changes in the model parameters (see OSM 3).

4. Discussion

The results of this model strongly suggest that worker ants responding to trail crowding by reducing pheromone deposition – crowding negative feedback (CNF) (Czaczkes et al., 2013b) – allows the maintenance of colony-level flexibility in a changing environment. When CNF was not implemented in the model ant colonies failed to refocus their foraging effort, regardless of PNF strength. This replicates results from other studies which did not include negative feedback (Nicolis and Deneubourg, 1999; Sumpter and Beekman, 2003). However, when a CNF with realistic parameters was implemented, colonies had managed to refocus their foraging effort in 97.6% of trials, averaged over all PNF strengths. This consequently has the effect of increasing the total amount of food retrieved by the colonies.

The mechanism behind the increased foraging flexibility is a reduction in the absolute strength of the pheromone trails produced. In later stages of foraging the CNF effect causes established trails to be barely strengthened. This means that when the environment changes, the small number of foragers discovering the newly high-quality food source can deposit a trail stronger than that leading to the established food source. It is noteworthy that while even extremely low levels of CNF result in dramatically reduced total pheromone levels at the end of each model run (Fig. 3), there is nonetheless a large difference between intermediate levels of CNF (Fig. 2). It is the effect of CNF at early stages of the model run that affects foraging flexibility. Dussutour et al. (2006) also demonstrate that crowding, at least in confined environments, can have an additional negative feedback effect by inducing ants to perform U-turns. This would conceivably also help counteract the positive feedback effect of trail pheromone following.

The flexibility reported here would naturally be beneficial to real ant colonies. However, in their classic paper Beckers et al. (1990) report that *L. niger* colonies failed to refocus their foraging efforts when a high quality feeder was presented once recruitment to a lower quality feeder was already underway. How can this contradiction between empirical results and the models' predictions be explained? One possible explanation can be found in the methodology used by Beckers et al.: colonies were presented with two feeders in an open arena. Thus, the paths which the ants took were unconstrained, and so individual workers may well have experienced few head-on encounters during their return journey. When foraging on nectar and aphid-patches ants must travel over thin branches, thus increasing their likelihood of performing head-

on encounters. Latty and Beekman (2013) also presented various ant species with two feeders of different quality, and then switched the two qualities once recruitment was well underway. However, in their experiment ants had access to the feeders via bamboo canes, thus restricting the paths to the feeders and increasing the number of head-on encounters. In both mass recruiting ant species tested the colonies began to refocus their foraging effort on the newly higher-quality feeder. Thus, it seems that the effect of the CNF effect may only become apparent on more natural, constrained trails. On the other hand ant-trails can often be seen to be closely constrained by the pheromone trail, resulting in many-head on collisions even in unconstrained environments (Sudd, 1960). This hypothesis is open to experimental testing. An alternative hypothesis is that lower-accuracy trail-following (i.e. noise) may help ant colonies refocus foraging efforts (Deneubourg et al., 1983; Dussutour et al., 2009a). A third possibility is that natural colonies and starved laboratory colonies differ in the variation of trail laying they demonstrate between high and low quality feeders. A bigger difference between the amount of pheromone deposited for good versus poor feeders will allow colonies to maintain foraging flexibility (De Biseau et al, 1991). While differential pheromone deposition for different food qualities has been repeatedly described in starved colonies (Beckers et al., 1992b; Jackson and Châline, 2007; Reid et al., 2013), the difference in pheromone deposition by starved colonies may be absolutely or relatively smaller.

The model demonstrates that the CNF effect is beneficial to ant colonies in the situation tested, and that a stronger CNF effect would not be of further benefit. The CNF effect also seems to come at a cost in terms of how fully the ant colonies could focus their foraging on the initial food source before the food qualities switched. When the CNF effect was enabled, a lower proportion of foragers were returning from the high quality feeder at time-step 1200, just as the feeder qualities were switched (see Fig. 4). Thus, there seems to be a trade-off between flexibility and decisiveness, or cohesion. Similarly, during house-hunting in *Temnothorax* ants, there is a trade-off between the speed of a decision into which new nest to move, and the cohesion of the colony (Franks et al., 2013). Perhaps the CNF strength in *L. niger* represents a compromise between flexibility and cohesion. Cohesion would be beneficial to colonies in competitive environments, where only by maintaining a large standing body of foragers on a food source could an ant colony dominate a valuable resource (Adams and Traniello, 1981; Holway, 1999; Lach et al., 2010). Moving from a CNF of 25 to that of 50 (the most realistic level) had a large effect on the proportion of trials with a successful refocussing for forager effort (from 71.4% to 97.6%). However, a further increase in CNF only resulted in very marginal gains (from 97.6% to 98.0%). This suggests that the realistic CNF effect strength has been tailored by natural selection to provide a good trade-off between colony-level flexibility and lack of cohesion. However, seen in another light a certain lack of cohesion may in fact be beneficial, as it allows information about poor food sources to be maintained, and therefore would allow colonies to better react to environmental changes similar to those modelled in this study. The optimal level of CNF, balancing colony decisiveness and cohesion against flexibility, will depend on the ecology of the specific ant species studied. It must be noted that as the model is only a rough approximation of ant foraging, I do not claim that my findings prove that the CNF levels used by real ants are optimal.

The results of the model suggest that pheromone negative feedback (PNF) – the effect where the presence of pheromone on a trail reduces further pheromone deposition (Beckers et al., 1992b; Czaczkes et al., 2013a) – does not play a major role in maintaining colony level flexibility. This is because the effect is in fact rather

weak when compared to CNF. With CNF disabled, a realistic PNF strength decreases total pheromone present at the end of the experiment by 73%. By comparison, with PNF disabled, a realistic CNF strength decreases total pheromone present at the end of the experiment by 95% (and see Fig. 4). One possibility is that PNF is used to prevent the wasting of metabolically expensive trail pheromone. However, when CNF is implemented at realistic levels the implementation of PNF at a realistic level only reduces total pheromone present by a further 1.2%, which may not be a strong enough effect to be favoured by selection. Another possibility, proposed by Beckers et al. (1992b), is that the PNF is an artefact caused by a further effect of trail pheromone; the increase of walking speed (Beckers et al., 1992b; Czaczkes et al., 2011). Thus, the apparently reduced pheromone deposition rates on area marked by trail pheromone may be caused by the ants walking faster on these areas, and thus leaving the area faster. The PNF effect may have emerged without being selected for, as a side-effect of the other effects of pheromone trails on ants.

The results of the model suggest that the implementation of a simple negative feedback rule can have great consequences for the flexibility of collective organisation systems based on positive feedback, such as ant foraging organisation. Negative feedback rules are of great importance for balancing and controlling organisation systems based on positive feedback (Detrain and Deneubourg, 2008). Much like real ant colonies, Ant Colony Optimization (ACO) meta-heuristics can also suffer from becoming trapped in local optima, and can be heavily influenced by the first random decision made during optimisation (Blum and Dorigo, 2004). Computer scientists have also implemented systems in order to avoid such early stagnation, which tellingly may include limiting either the maximum or minimum amount of pheromone on a path (Jovanovic and Tuba, 2013; Wong and See, 2009). Another tantalising parallel to the behaviour of real ants is the recent implementation of a rule in which pheromone deposition is up-regulated in underused areas of a network (Wong and See, 2009). Lastly, stagnation can be avoided by retroactively removing pheromone on undesirable parts of the matrix (Jovanovic and Tuba, 2011). While some of these methods, such as the retroactive removal of pheromone, may be impossible for ants (but see Robinson et al., 2005), some of the techniques developed by computer scientists may well have already been evolved by ants. Conversely, the simplicity of the negative feedback systems described in this paper may make it attractive for implementation in ACO, as the processing costs it involves would be minor, and the benefits potentially large. This model has demonstrated that the addition of such a negative feedback system can add increased functionality to a system with only a low cost in terms of decisiveness.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2014.07.005.

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