ESM 4 - Sensitivity analysis

Contents

Introduction to the sensitivity analysis

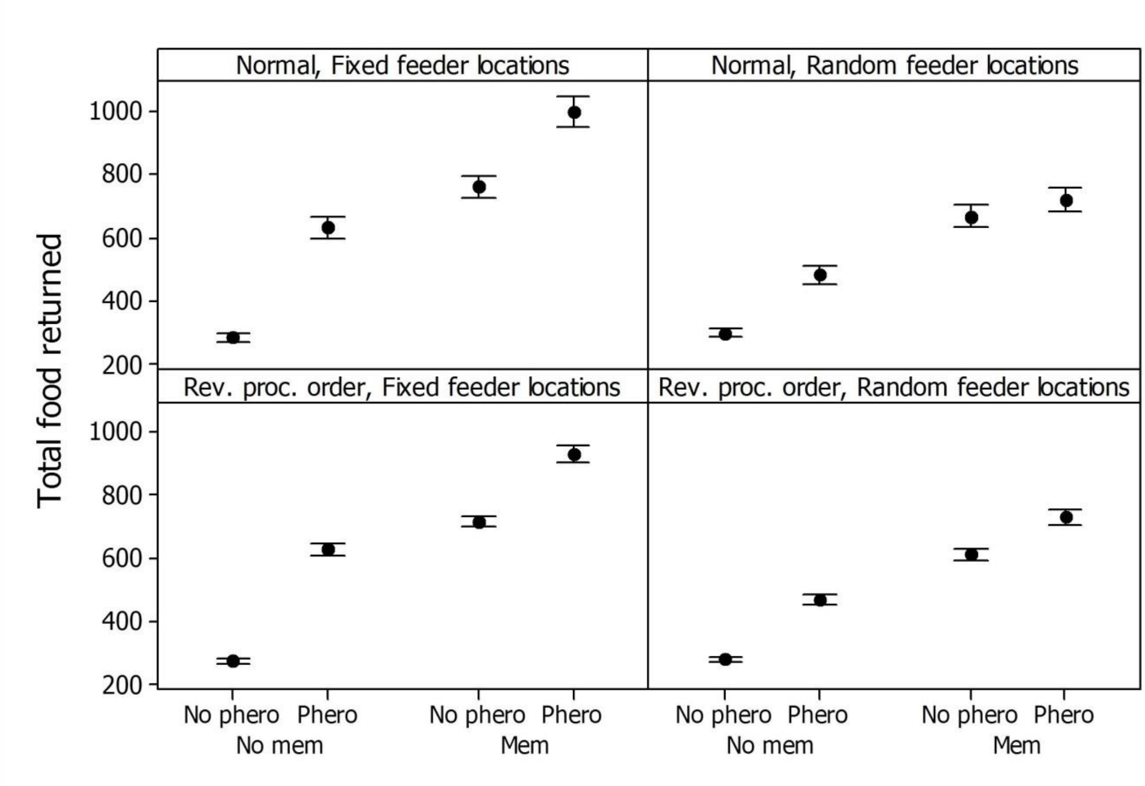
There are several variables and parameters in the model which, while not being directly relevant to testing our hypotheses, may have influenced the results of model. Such variables include the procedure order, the world size, the rate at which the pheromone evaporates, the variability of the ant's correlated random walk, the number of time steps the model runs for, and whether a crowding negative feedback effect on pheromone deposition is enabled. These were systematically varied, and their effect on the collective behaviour of the ant colonies examined. To save processing time, only 250 runs of each unique combination of variables were performed. The variables not being varied were maintained at the level used in the main analysis. Variable effects tested for in the main analysis were fixed as follows:

- Number of feeders - 16
- Maximum memory - 15
- Rate of environmental change - every 2000 ticks
- Waiting time at an empty feeder - 30 ticks

We present the effect of the sensitivity on the most salient measure of collective behaviour for the model – total food returned by the end of the model run.

Reversed procedure order

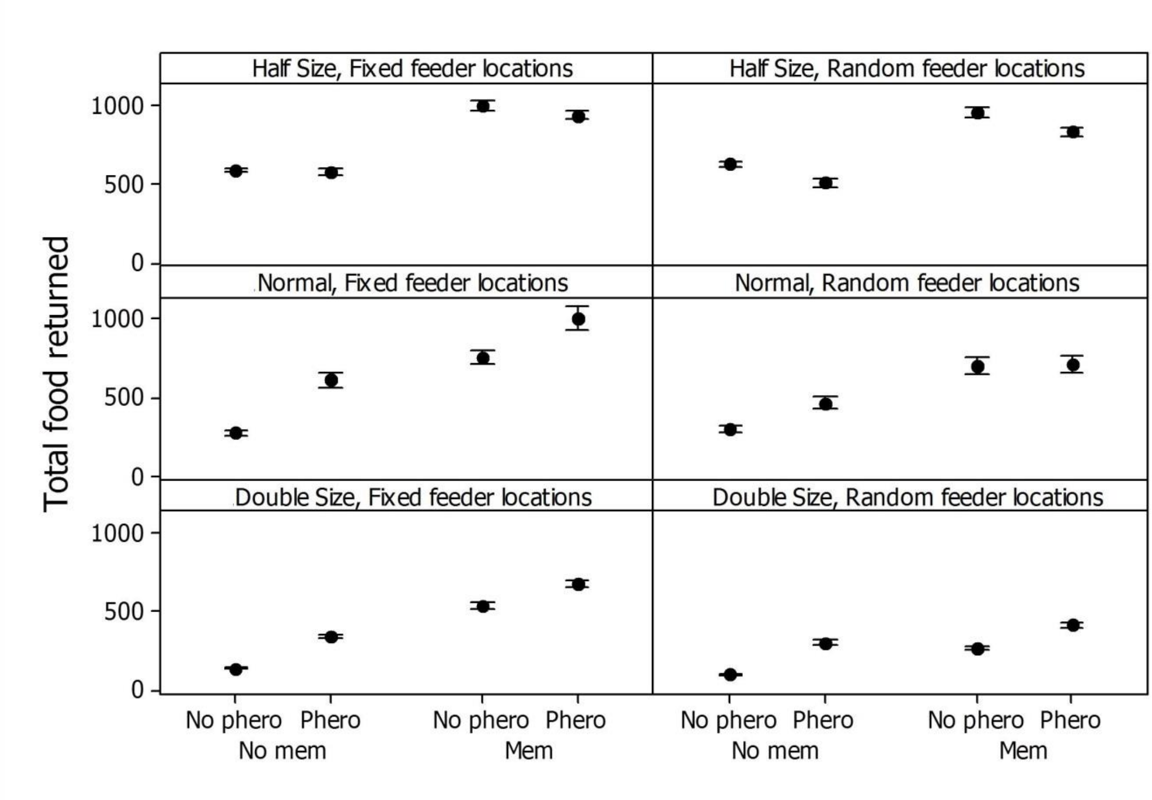
The order in which the main procedures in the programme are called was reversed. This had no effect on the model.



Word size

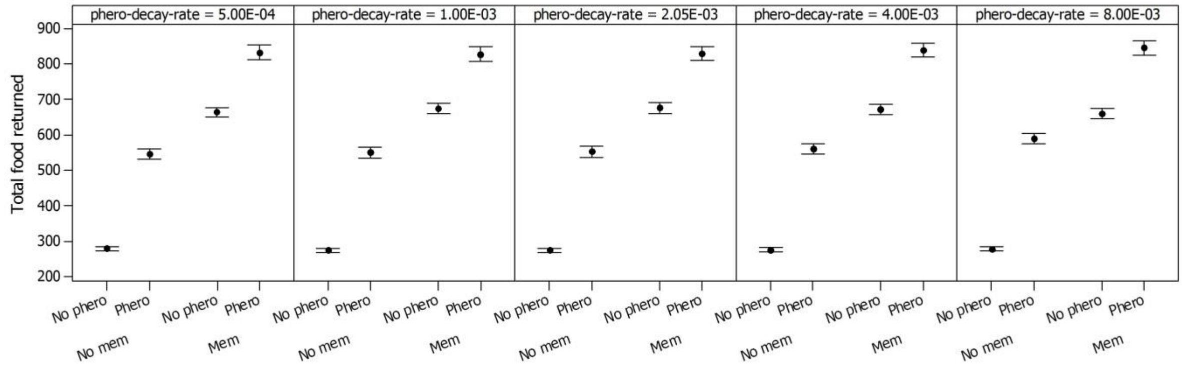
The world size was either doubled (400x400 patches) or halved (100x100 patches).

The main result, of a complementary effect between pheromone and memory, remains stable of is strengthened in larger worlds. In the half-sized world where feeder locations are random pheromone trails can slightly hinder colony-levels foraging, as overlapping trails 'hide' other trails.



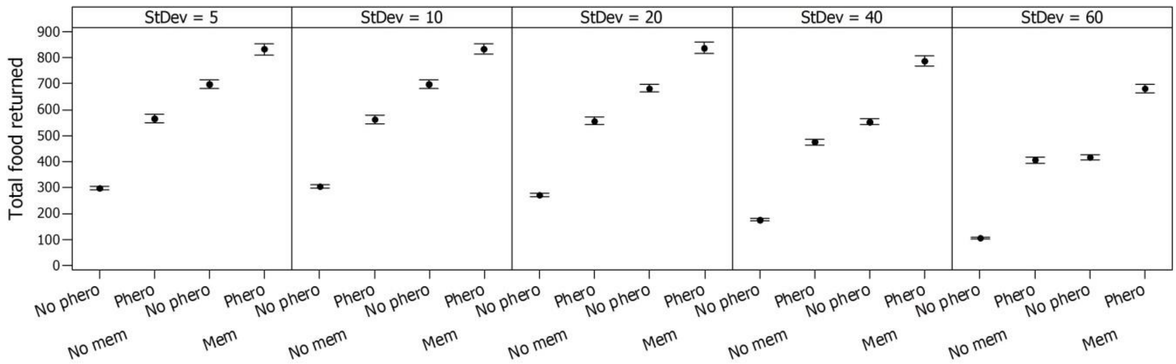
Pheromone evaporation rate

Here, we systematically varied the rate at which pheromone evaporates. This had no effect on the results of the model.



Variability of the agents' correlated random walk

In the model, the agents perform a random walk by drawing a random number from a distribution with a mean of 0 and a standard deviation of StDev (set at 20 for the main analysis), and turning left by this amount (negative numbers cause the agents to turn right). Here, we systematically varied StDev. This had no major effect on the results of the model.

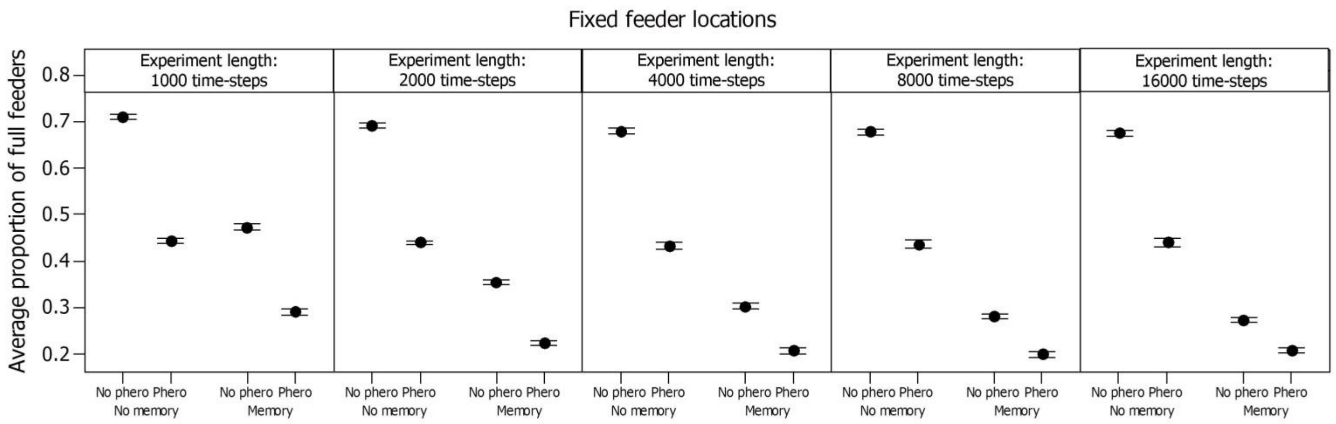


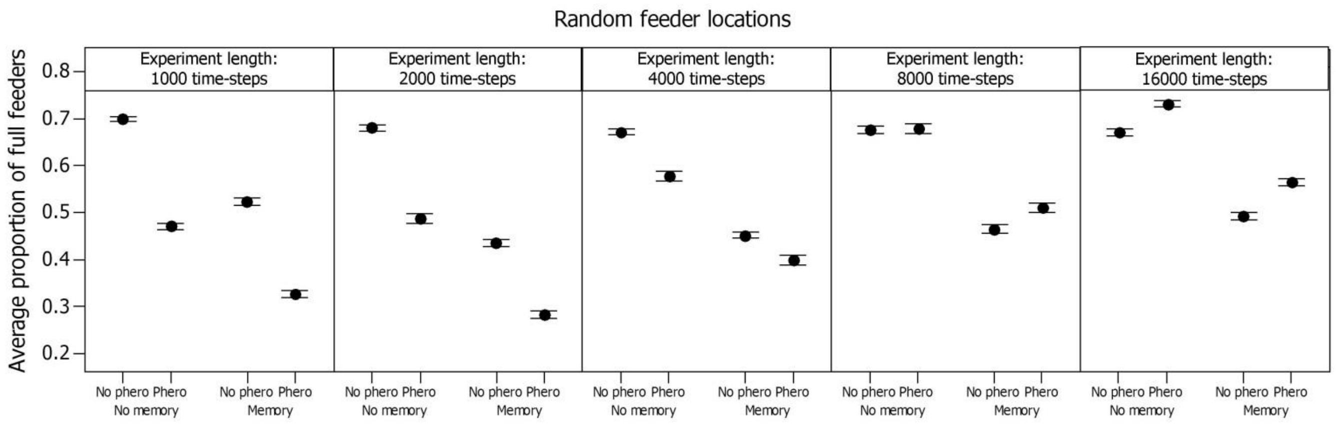
Experiment length

In the main experiment each model ran for 4000 time steps. Here, we ran the model for 1000, 2000, 4000, 8000 or 16000 time steps. Since total food retrieval is affected by how long the ants have to collect food, we present the average proportion of full feeders as a measure of colony level performance. Lower values represent higher efficiency at exploiting the environment. This measure correlates very well with total food retrieval given fixed experiment lengths.

As experiment time increases, memory becomes more effective, as can be seen when only memory is available. This suggests that the ants are distributing themselves more effectively as time progresses. This pattern can also be seen when pheromone is also available, but the pattern is dampened as the efficiency of the colonies is approaching total efficiency.
The general pattern of a complementarity between pheromones and memory is maintained.

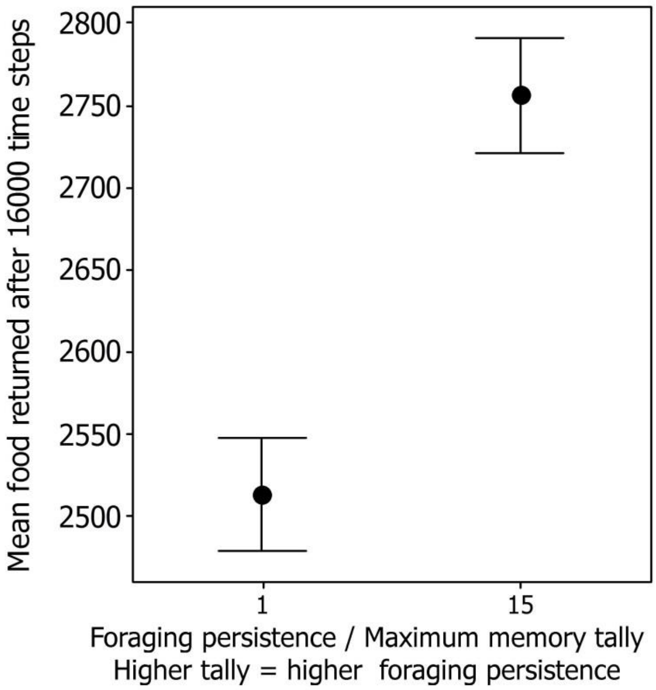
When feeder locations are random, complementarity between pheromone and memories erodes, with pheromones eventually becoming a hindrance to colony efficiency. This mirrors the effect of a highly variable environment (see results in main text).





The effect of foraging persistence in longer model runs

The results of the sensitivity analysis exploring model running time indicated that, given longer running times, memory can allow greater foraging efficiency. However, only realistic memory based foraging persistence is modelled. To explore the effect of foraging persistence further, we modelled ants with realistic (15) or low (1) foraging persistence, in models that ran for 16,000 time steps. When realistic foraging persistence is implemented, 9.67% more food is retrieved after 16,000 time steps than with low foraging persistence.



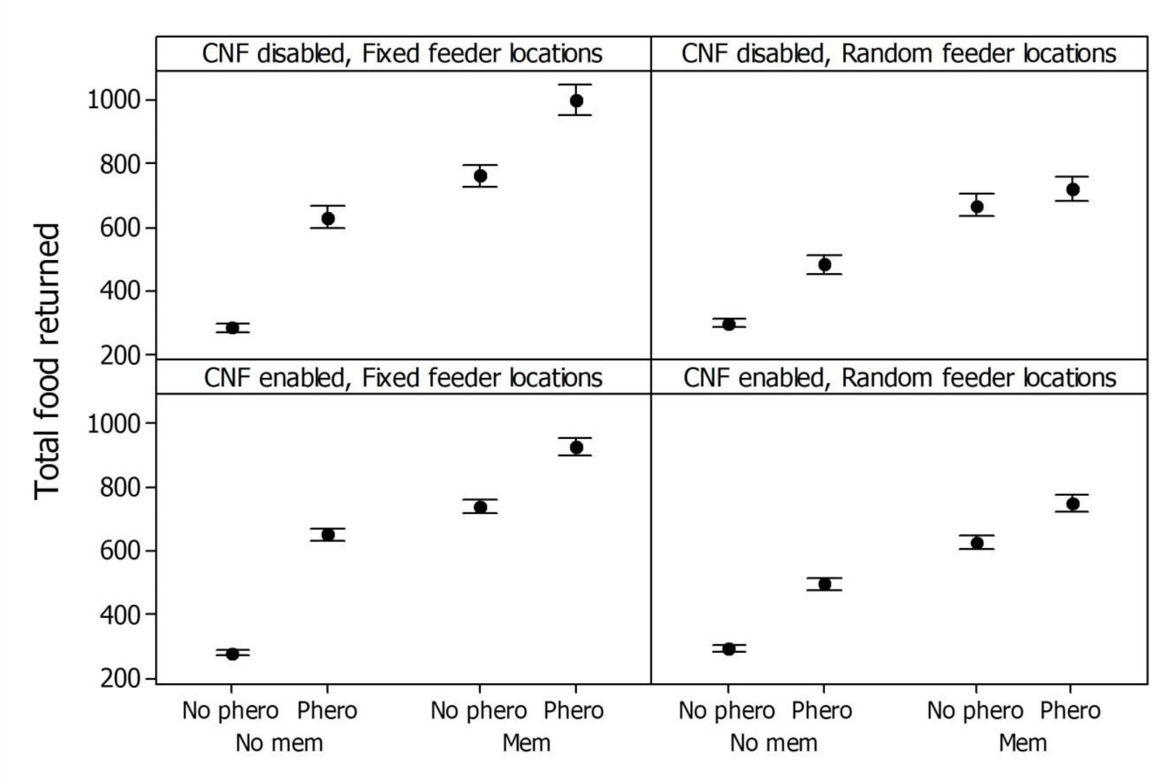
<u>Crowding negative feedback</u>

Czaczkes et al. (2013; 2014) demonstrated that ants which encounter other ants on a trail strongly reduce their pheromone deposition rate. Czaczkes (2014) demonstrated that such a negative feedback effect could have large implications for colony-level behaviour. To test whether such a negative feedback effect may affect our results, the negative feedback effect used in Czaczkes (2014) was incorporated into the model, as follows: every time an ant encounters another ant it increases its' 'crowding' tally by one. This tally is reset when the ant reaches the nest. Pheromone deposition is reduced in relation to this tally, at a rate parameterised by empirical data from Czaczkes et al (2013), using the equation:

$$P_{laid} = \frac{F_{quality}}{CNF \ \times 0.004 \ \times crowding + 1}$$

Where $F_{quality}$ is the quality of the food source in terms of sucrose concentration – in the current experiment always set to 50.

Enabling crowding negative feedback has no effect on the main results of the model.



References mentioned in this supplement

Czaczkes, T. J. (2014). How to not get stuck–negative feedback due to crowding maintains flexibility in ant foraging. *Journal of Theoretical Biology*, *360*, 172–180. doi:10.1016/j.jtbi.2014.07.005

Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. W. (2013). Negative feedback in ants: crowding results in less trail pheromone deposition. *Journal of The Royal Society Interface*, *10*(81). doi:10.1098/rsif.2012.1009

Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. W. (2014). Rapid up- and down regulation of pheromone signalling due to trail crowding in the ant *Lasius niger*. *Behaviour*, *151*(5), 669–682.