

Description of the group selection model

The model, a haystack-style simulation of group selection¹, was constructed to capture the essential features of colony foundation for queens of the ant *Pogonomyrmex californicus*. The life history features of this species during colony founding match in many details the haystack thought experiment of Maynard Smith¹: randomly distributed queens aggregate to found nests^{2,3} with some queens being cooperative in behavior and others aggressive^{3,4} (variation in this aggression is also described in detail in our empirical data. As shown by our empirical data, aggressive queens survive longer (at the expense of more cooperative nest-mates), but groups composed purely of cooperators survive much longer individually (and as a group) than groups containing aggressive individuals. The goal of this model is to generate testable predictions relevant to the hypothesis that this system fits the haystack scenario of group selection as an explanatory model for the observed queen cooperation in this natural population. Our model was implemented using the modeling environment Netlogo⁵.

Given is a torus shaped landscape of $N \times N$ cells (100 x 100 cells in our simulations). Each cell is a suitable location for a colony with probability p_s . Agents represent queens starting nests. Queen mortality comes from inter-queen fights, not other causes (hence this limits the size of the queen population).

At the start of each new iteration of the model, there are m new queens. This means a density of $\frac{m}{N^2}$ queens per cell, and $\frac{m}{N^2 \cdot (1-p_s)^2}$. Queens can be cooperative (defined behaviorally for the model as non-aggressive) or fierce. The initial share of cooperative queens is x_{C0} .

Queens are distributed randomly on the landscape and then cluster with others within a given radius, r_C to the best colony spot on the landscape; this location is defined as the cell with the most other queens on it⁶. The position of the queens is updated in a random order. Foundresses of this species in the Lake Henshaw and Pine Valley populations (the subjects of our empirical study) have been shown to aggregate regardless of population of origin^{3,5}.

After the clusters are defined, each cell with more than one queen evaluates if there are any fights between queens. In random order the model updates a pair of queens. A fierce queen has a probability p_I to initiate fights. When two queens are cooperative they do not initiate fights. When a fight is initiated one of the two queens dies. If both queens are fierce each queen has a 50% probability to die. If one queen is fierce, the cooperative queen has a probability p_{DC} (=60%), and a fierce queen has probability p_{DF} (=40%) to die. Estimates for probability of mortality are based on mortality outcomes in empirical data^{1,4}. At the conclusion of these within-colony interactions some number of queens remain alive in the group.

When the queens are finished with their internal fights, the effect of inter-group competition is evaluated. Each colony evaluates which other colonies overlap in territory where the territory is defined within a radius r_G . The probability of a colony to survive the competition is based on the productivity function of Bartz and Hoelldobler^{1,7}:

$$s(x) = -2.88 + 4.28 \cdot x - 0.377 \cdot x^2$$

Where x is the number of queens and $s(x)$ is the worker production function (Figure 1). In competition with other groups, the production function is tantamount to survival. We use the function to define the competitive potential of each queen group. Based on the relative values of the survival function of group 1 vs group 2 ($s(x_1)$ vs $s(x_2)$), the probability that x_1 wins the competition - leading to the death of all queens from nest 2 is equal to $s(x_1)/[s(x_1)+s(x_2)]$. *Pogonomyrmex* foundress associations have a similar production function as the species documented by Bartz and Hoelldobler (unpublished data). A similar function has also been reported in fire ants^{2,3,6}.

We assume that colonies who are closer to each other are first to experience the effect of competition. As such the order in which colonies are updated is in the order of the distance between two colonies. At the end of the competition between colonies, no colonies overlap in their territories.

Finally the probability of cooperative or fierce queens for the next generation of m queens is calculated. Each colony is allocated the same share of offspring to the next generation, regardless of the number of queens in the colony. For each colony the share of cooperative and fierce agents are calculated, summed over all colonies - which leads to a relative share of cooperation at the landscape level. Now m new queens are generated with a probability being a cooperative queen equal to the relative share of cooperation. For example, with a global reproduction of 100, if 10 nests survive to reproduce – each nest will be allocated 10 queens for the next generation (regardless of whether there is one or several queens present in each nest). For each nest, the offspring will be allotted proportional to type. A nest composed of three cooperators and two fierce queens would then produce 6 cooperators and 4 fierce offspring. Another nest composed of a single fierce queen would be allotted 10 fierce offspring in the next generation.

After reproduction the mature colonies are removed and the model protocol repeats. Finally, with a probability of p_m each queen can switch to the other type. In Table 1 we show the parameter values for our simulations unless otherwise indicated.

	Description	values
N	Dimension of landscape	100
m	Number of new queens	100 - 1500
x_{C0}	Initial percentage of cooperative queens	5
r_C	Radius for clustering of queens	1-10
r_G	Radius for group competition	1-10
p_I	Probability a fierce queen initiate fighting	0 -1
p_s	Probability that a cell is suitable for a colony	1
p_m	Probability of mutation	0.01
p_{DC}	Probability that a cooperative queen dies in a fight	0.6
p_{DF}	Probability that a fierce queen dies in a fight with a cooperative queen	0.4

Table 1. Here we show the range of parameter values explored in the model.

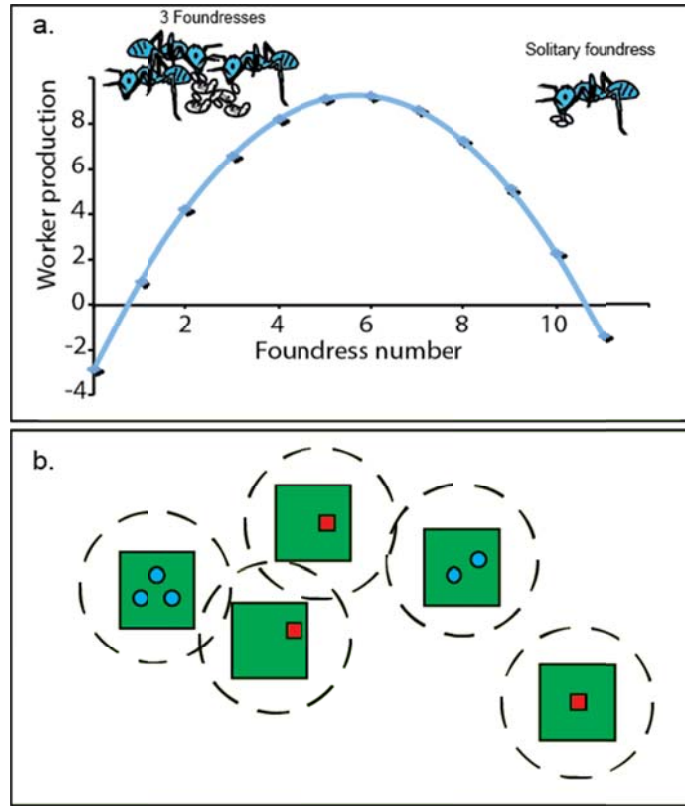


Figure 1. a). In pleometrotic species of ants, cooperative colony founding results in the production of more workers relative to solitary founding. The plot shows the function determined in Bartz and Hoelldobler^{3,4,7}. b). During colony founding this advantage in production is tantamount to survival when competition between new colonies is intense. Though it has not been documented in our study species, *P. californicus*, fire ants and honeypot ants demonstrate brood raiding^{6,7} – whereby the foundress groups with the first young workers (minims) raid and destroy less well established neighbors. Our model uses the production function as a proxy for competitive ability.

Process overview:

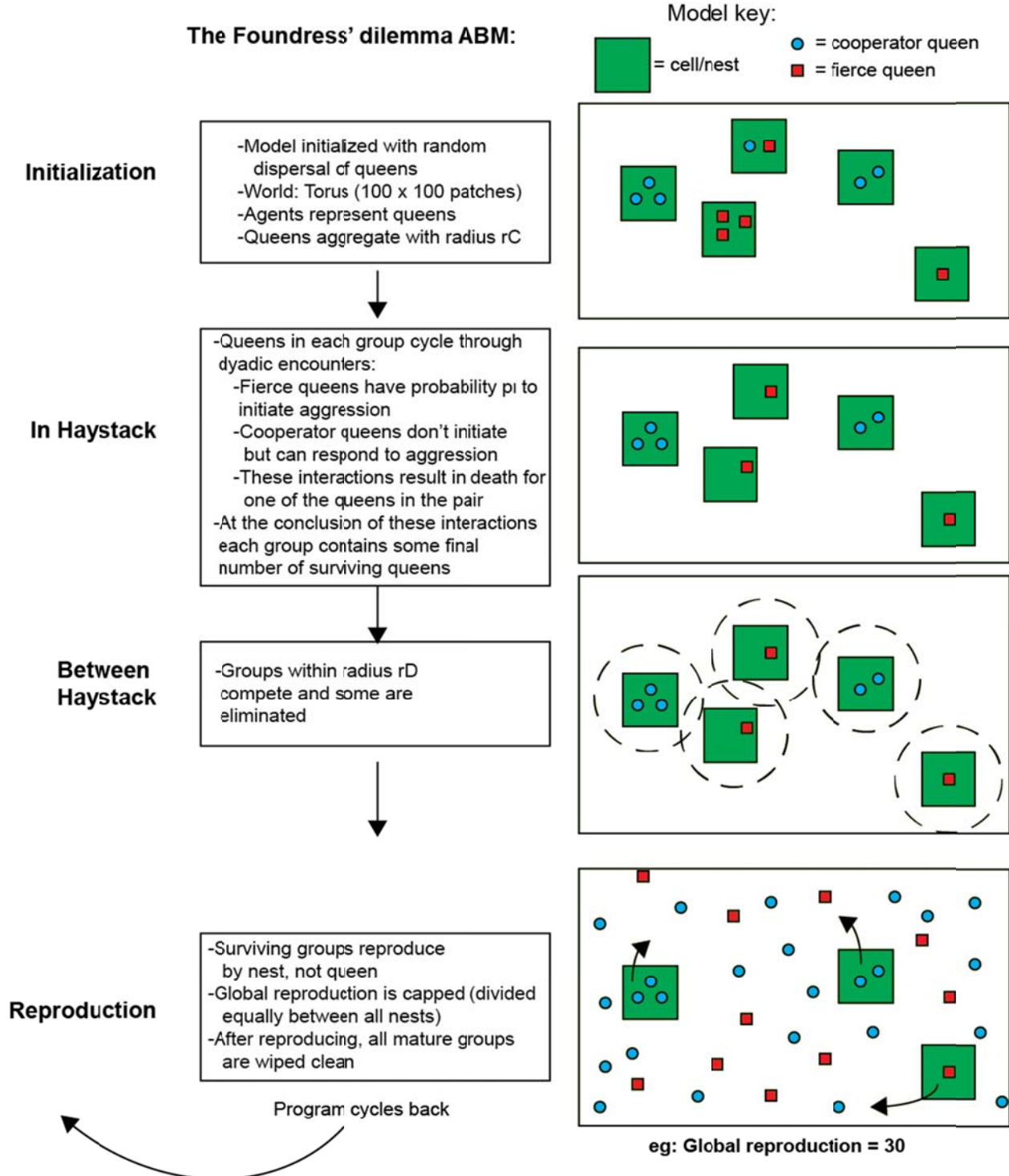


Figure 2: Process overview for the simulation

Model results:

The result is shown below for three population sizes: 500, 1000, and 1500 queens. Clustering, competition, and population size interact with one another to influence the threshold where cooperation dominates. Increasing population size has the effect of shifting this threshold forward such that the transition to cooperation occurs at lower clustering and competition distances.

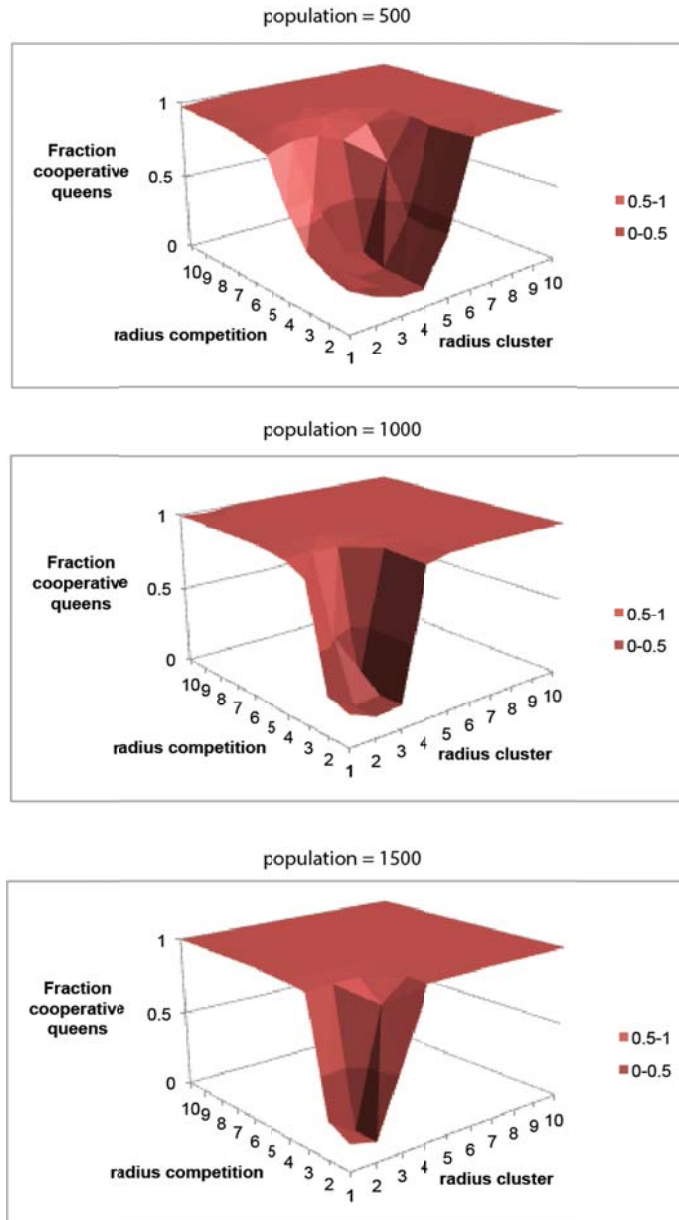


Figure 3: Fraction of cooperative queens evolved in 100 simulation for each combination of radius competition (r_G) and radius cluster (r_C) for three different population sizes, 500, 1000, and 1500 queens, respectively.

Because the radius of clustering and the radius of competition had a similar effect on the success of cooperative agents, in some analyses we pegged the two at the same value. We found little effect by changing the probability of initiating aggression (for fierce queen-agents). Below we show this for a population of 1000 queens (Figure 4). Each line shows a different probability for initiating aggression. The higher the probability of initiating aggression, the steeper the change from non-cooperative to cooperative queens with increasing radius levels. In Figure 5 we show that the transition to cooperative queens happens with smaller radius when the population numbers are larger.

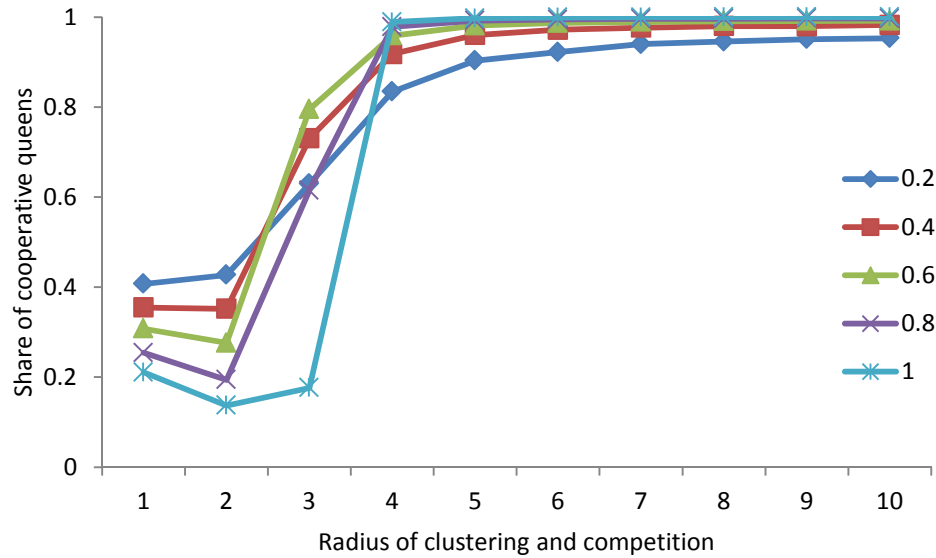


Figure 4. Share of cooperative queens as an average of 100 simulations for each combination of radius size and probability of initiating aggression by fierce queens.

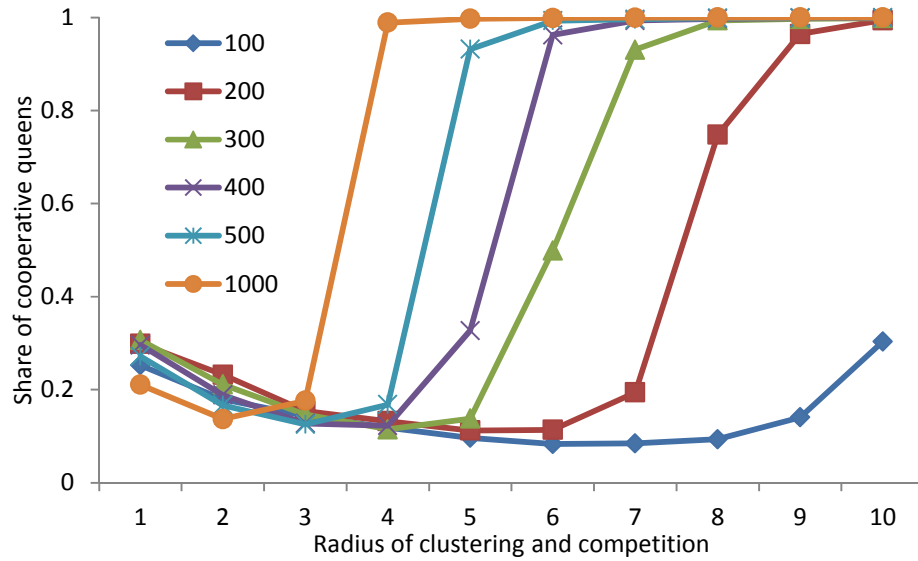


Figure 5. Share of cooperative queens as an average of 100 simulations for each combination of radius size and group size.

Below is the distribution of group sizes for different radius levels (4,-10), where the radius cluster for clustering and competition are assumed the same. For radius levels 1-3 more than 97% of the colonies have only one queen. For radius 4 and higher 70% of the colonies have more than one queen.

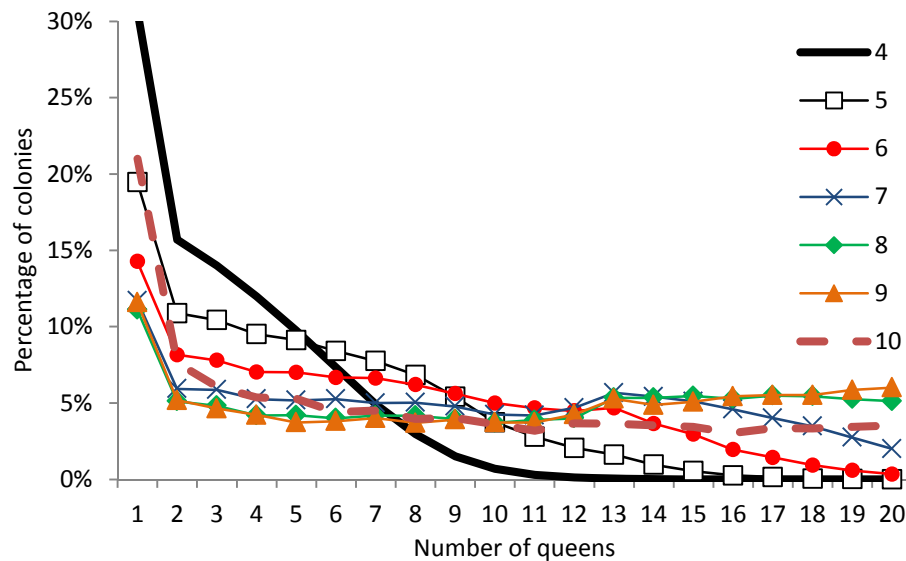


Figure 6. Share of the colonies who have a certain number of queens for different level of radius (where the radii of clustering and competition are pegged to the same value).

References:

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5. Wilensky, U. {NetLogo}. (1999).
6. Tschinkel, W. R. & Howard, D. F. Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. *Behavioral Ecology and Sociobiology* **12**, 103–113 (1983).
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