The Power of Population Effect in Temnothorax Ants House-Hunting: A Computational Modeling Approach

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Running Head: Population Effect in Temnothrorax House-Hunting

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Abstract: The decentralized cognition of animal groups is both a challenging biological problem and a potential basis for bio-inspired

design. In this study, we investigated the house-hunting algorithm used by emigrating colonies of *Temnothorax* ants to reach consensus on a new nest. We developed a tractable model that encodes accurate individual behavior rules, and estimated our parameter values by matching simulated behaviors with observed ones on both the individual and group levels. We then used our model to explore a potential, but yet untested, component of the ants' decision algorithm. Specifically, we examined the hypothesis that incorporating site population (the number of adult ants at each potential nest site) into individual perceptions of nest quality can improve emigration performance. Our results showed that attending to site population accelerates emigration and reduces the incidence of split decisions. This result suggests the value of testing empirically whether nest site scouts use site population in this way, in addition to the well-demonstrated quorum rule. We also used our model to make other predictions with varying degrees of empirical support, including the high cognitive capacity of colonies and their rational time investment during decision-making. Additionally, we provide a versatile and easy-to-use Python simulator that can be used to explore other hypotheses or make testable predictions. It is our hope that the insights and the modeling tools can inspire further research from both the biology and computer science community.

1 Introduction

Animal groups are capable of remarkable displays of highly coordinated behavior. Fish schools collectively choose foraging sites (Ward et al. 2012), locusts self-organize into orderly swarms (Yates et al. 2009), oceanic fish assemble in

vast migratory shoals (Makris et al. 2009), and social insects perform a host of collective actions including group foraging, construction of complex nests, and adaptive allocation of tasks across the labor force (Charbonneau et al. 2015; Detrain et al. 2008; Detrain et al. 2019; Oldroyd et al. 2015; Perna et al. 2017; Seeley 1995). How these group actions result from individual behavior remains a major research challenge. Although well-informed leaders may play a role, group organization is typically very decentralized (Detrain et al. 2008; Feinerman et al. 2017; Seeley 1995). Coordination emerges from interactions among large numbers of animals acting on limited local information with appropriate decision rules. Connecting individual behavior to group outcomes is too much for unaided intuition, hence mathematical models and agent-based simulations have become useful tools for understanding. In this paper, we present a model for a notable example of decentralized decision-making: nest site selection by ants of the genus *Temnothorax*.

Models, in combination with experimental studies, have already revealed much about these ants, making them a leading study system for collective decision-making (Pratt 2019). Colonies live in pre-formed cavities such as rock crevices or hollow nuts; if their home is damaged, they are adept at finding candidate new homes, evaluating each site's quality, and moving the entire colony to the best one. Their decision emerges from the separate efforts of many scouts, each independently recruiting nestmates to the site she has found. Because recruitment is quality-dependent, better sites accumulate ants more rapidly (Mallon et al. 2001). These differences are amplified by a quorum rule under which scouts accelerate recruitment to a site once its population crosses a threshold; the winner of the race to attain a quorum becomes the colony's choice (Pratt et al. 2002). An agent-based model has shown that this algorithm helps the colony reach consensus on the best site (Pratt et al. 2005). Other models have

shown how a colony can make a good choice even when no individual directly compares sites (Masuda et al. 2015a; Robinson et al. 2011), and how individual behavioral strategies optimize speed/accuracy tradeoffs at the colony level (Franks et al. 2013a; Marshall et al. 2006; Marshall et al. 2009; Planqué et al. 2007; Pratt et al. 2006; Sumpter et al. 2009).

Although successful, models that are based on biological measurements can easily become intractable and hard to use for new predictions. Consequently, most model predictions have been limited to the simple challenge of choosing between two distinct and equidistant nests in a controlled laboratory environment. Real colonies face more complex scenarios, such as selecting among several sites of varying quality, avoiding splits when candidate nest sites are identical, and resolving colony splits when they occur (Doering et al. 2019; Sasaki et al. 2012). It also remains unclear how the colony maintains high performance with noisy and heterogeneous individuals, and how individuals modify their behavior to account for changes in context or colony state. In addition, a large body of experimental work has uncovered new colony behavior that has yet to be explored in terms of how well our current understanding of the ants' collective algorithm can explain them. These include the more complex scenarios mentioned above, as well as effects on decision-making of colony size and emigration distance, colony reconnaissance of potential new homes, and the emergence of group-level rationality despite individual-level irrationality (Franks et al. 2008; Sasaki et al. 2011; Stroeymeyt et al. 2010).

To better capture the complexities of nest-site selection, we develop a tractable model for the analysis and exploration of the underlying behavioral algorithms. We show that the model can reproduce individual and collective behavior in published studies of simple one- and two-nest experiments. For these data, our model performed similarly to an earlier agent-based model that inspired our

work (Pratt et al. 2005).

We then used the model to explore beyond known features of the ants' behavior. In particular, we tested the hypothesis that scout ants attend to a site's population when deciding whether to recruit to it, such that the probability of recruitment increases with population. This hypothesis is different from the well-established quorum rule, under which a recruiter switches from one kind of recruitment (tandem run) to another (social transport) on the basis of site population. Rather than determining the type of recruitment, the proposed population effect is about the ant's decision whether to recruit at all. The reason to suspect this population effect is its potential role in preventing splits or stalemates when a colony is faced with a choice between very similar nest sites. Without some rule to break the tie, the colony might be unable to reach consensus. A population effect on site evaluation could provide such a tie-breaker, because random differences in discovery and recruitment could easily produce a population difference between competing, identical sites. If scouts then show enhanced recruitment to the site that had the larger population, this would amplify the difference, creating positive feedback that could direct the emigration entirely to whichever site happened to take an early lead in population.

To explore this idea, we ran our model with different strengths of population effect to determine how it affected a colony's ability to decide between two identical nests, a context that poses a particular challenge to consensus formation. As described below, our results confirmed the hypothesized population effect on both emigration speed and consensus. Finally, we extended the model to account for more recent empirical observations on robust decision-making among larger numbers of options (Sasaki et al. 2012) and rational colony decisions about decision speed (Sasaki et al. 2019).

The rest of the paper is organized as follows: Section 2 introduces our agent-based model for the house-hunting process and the main hypothesis we test: the population effect. Section 3 describes our model parameters and the performance metrics that our predictions about the population effect are based on. Then Section 4 showcases simulation results that confirm the population effect hypothesis. This suggests the value of empirical measurements of population effects, despite the experimental difficulties. Next, in Section 5, we use the model to test or extend other hypotheses that have varying degrees of support from newer empirical studies. Finally, in Section 6, we summarize our results and discuss future work directions.

2 House Hunting Model

2.1 Informal Description

A *Temnothorax* colony is composed of adult workers and brood items (immature ants), each group making up 40% to 60% of colony members. Adults are roughly equally divided between active workers, who organize and execute emigrations, and passive workers, who, like brood items, are typically transported to the new nest by active workers and do not themselves recruit nestmates (Pratt et al. 2005; Dornhaus et al. 2008; Valentini et al. 2020a).

There are four distinct phases for an active worker in the house-hunting process. In the first, the **Exploration** phase, the ant randomly starts to explore her surroundings for a suitable new nest. If she finds a candidate site, she enters the **Assessment** phase, where she individually assesses the site's quality according to various metrics (Healey et al. 2008; Franks et al. 2003; Pratt 2005b). If she judges the site to be satisfactory, the ant accepts it and enters the **Canvassing** phase, in which she returns to the old nest to recruit

other ants to the site by leading *forward tandem runs* (FTR). In a FTR, the recruiter slowly leads a single follower (another active worker) from the old nest to the new (Moglich 1978; Richardson et al. 2007; Valentini et al. 2020b). Upon arriving at the nest, the follower ant goes directly into the Assessment phase and evaluates the nest's quality independently of the leader ant. If she finds the nest satisfactory, she will transition to the Canvassing phase and start leading FTRs to the nest. A canvasser continues leading FTRs until she perceives that the new nest's population has exceeded a threshold, or quorum (Pratt 2005c). At this point, she enters the **Transport** phase, in which she fully commits to the new nest as the colony's home. She ceases FTRs and instead switches to picking up and carrying nestmates from the old to the new nest. These transports are faster than FTRs, and they are largely directed at the passive workers and brood items, hence they serve to quickly move the entire colony to the new nest (Pratt et al. 2002; Pratt et al. 2005). Previous models and experiments indicate that the quorum rule helps the colony to reach consensus rather than splitting among multiple sites (Pratt et al. 2002; Franks et al. 2006; Franks et al. 2013b). Splitting becomes a danger if ants at different sites, each ignorant of their nestmate's discoveries, launch FTRs to their respective sites. The quorum rule makes it likely that whichever site first hits the threshold will quickly end up with all or most of the colony, due to the speediness of transport.

Although experimental evidence is equivocal, we assume that the quorum size is correlated with the number of adult workers in the colony (Dornhaus et al. 2006; Franks et al. 2006). We also assume that passive workers can contribute to quorum attainment. Once the quorum is met, the switch to Transport phase is irreversible: an ant continues transporting nestmates to her new home nest even if the nest population later drops below the quorum size (Pratt 2005c). However, transporters do sometimes interrupt transport to search for and assess

alternative nest sites. If the search yields a new site that is better than the ant's current nest, then she exits the Transport phase and enters the Assessment phase with the new site as her candidate nest.

An ant in the Canvassing or Transport phase does not recruit indefinitely. Once the site from which she is recruiting is empty, she returns to her home nest and transitions back to the **Exploration** phase. However, this happens only upon meeting a "termination" condition consisting of ten occurrences of either of the following events: 1) the worker tries to lead a FTR where the solicited follower is also trying to lead her own FTR, and 2) the worker tries to carry another worker who is also in the Transport phase. This condition is based on frequent observation of these events at recently emptied nests. We hypothesize that an ant's requirement of several such events is a means of ensuring thorough exploration of the old nest so that no nestmates are left behind. We do not have a precise measure of how many such events are required, but chose the number ten as an upper-bound estimate.

Unlike active worker scouts, passive ants and brood items remain in the old nest until they are carried to the new nest. The only difference between passive ants and brood items is that the former contribute to quorum attainment (Pratt et al. 2002; Dornhaus et al. 2008). Therefore, in our model, the only states for any passive ant or brood item is her location and her role of being passive or brood.

The emigration is completed when all ants in the colony are relocated to the new nest, except possibly for a few active scouts (Pratt et al. 2002).

2.2 Modeling Techniques

In this section, we summarize the modeling techniques in this paper. However, we are including only a high-level overview in this section, and more details can

be found in the Appendix A and B.

We develop an agent-based model, where each ant is an agent and is modeled by its own state machine. We use a discrete and synchronous timing model, where time is divided into discrete rounds, and all agents enter a round together. In a round, each agent gets a chance to perform at most one state transition.

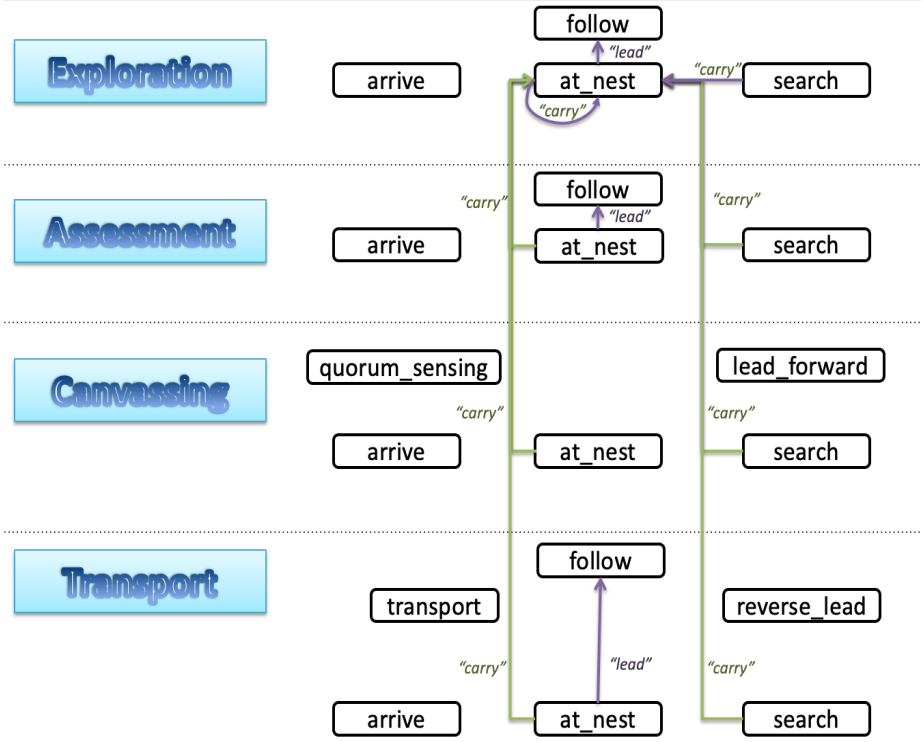
Apart from agents, another model component is the environment, containing one home nest and at least one candidate nest. Each nest has its own physical quality.

Agents can transition from one state to another, by initiating an action or receiving an action. Variables representing an agent's state are divided into two parts: external state variables that are visible to other ants, and internal state variables that are only visible to the agent itself. All state variables can change due to a transition. Fig. 1 show the changes of two important external state variables, *state_name* (in black boxes) and *phase* (blue filled boxes on the left), due to each action (arrows). The changes of other variables due to these transitions can be found in Appendix B.

2.3 The Population Effect Hypothesis

Under this hypothesis, for individual decisions that depend on assessing a nest's quality, the assessment includes both its physical qualities (Burns et al. 2016; Sasaki et al. 2015) and the nest population (Pratt 2005d; Dornhaus et al. 2006). Therefore, with inspirations from (Ghaffari et al. 2015), in Fig. 1b we model the final nest quality x as a simple linear combination of these two factors, with a new parameter called **pop_coeff** as the coefficient of the population. In other words, the final nest quality of a nest with physical quality q and population *pop* is

$$\frac{q}{4} + \textbf{pop\_coeff} \times \frac{pop}{num\_ants}, \tag{1}$$



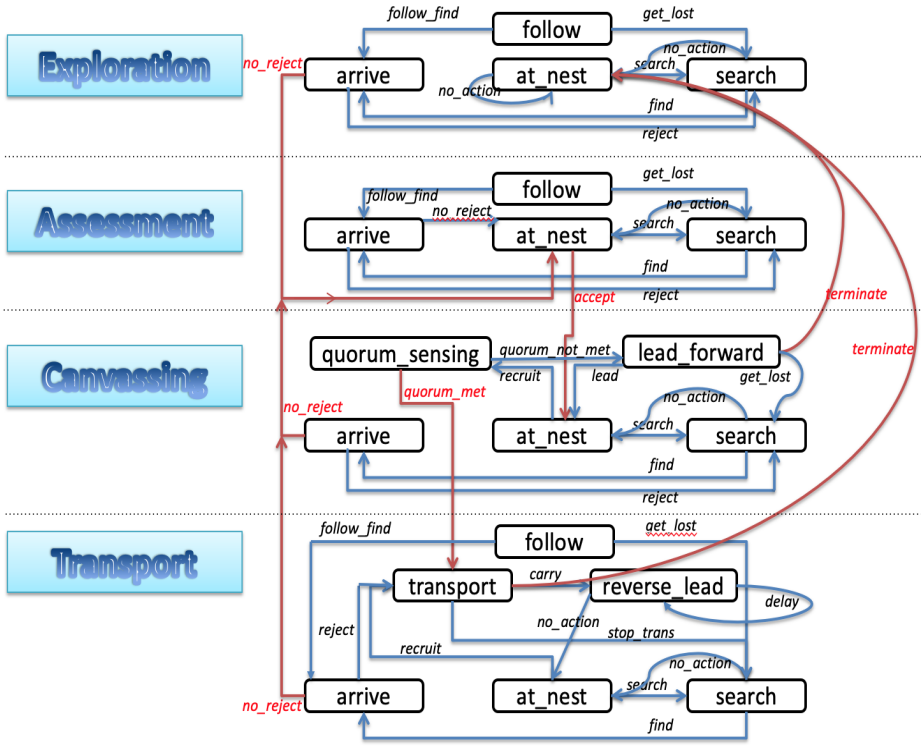
(a) *Action-types* an active ant can receive from another ant and the corresponding *state_name* and *phase* transitions.

Figure 1: States and actions modeling the behavior of active ants responsible for organizing colony emigrations. As described in Section 2.1, the four distinct phases are in different boxes: Exploration, Assessment, Canvassing, and Transport.

where 4 is the maximum value of nest qualities, and *num_ants* is the total colony size. We further define the following sigmoidal function (Fig. 2)

$$p(x) = \frac{1}{1 + e^{-\lambda \times x}}, \tag{2}$$

where λ is a parameter that controls how "steep" the sigmoidal function is, and x is the above defined nest quality. Higher λ values correspond to lower individual noise level. A lower individual noise level (higher λ) means that



(b) *Action-type*'s an active ant can initiate and the corresponding *state_name* and *phase* transitions.

Figure 1: (Cont.) States and actions modeling the behavior of active ants responsible for organizing colony emigrations. As described in Section 2.1, the four distinct phases are in different boxes - Exploration, Assessment, Canvassing, and Transport.

there is a higher chance that an ant can tell that a good nest is good and a bad nest is bad, and makes the "correct" individual decision to move the emigration forward through the four phases.

Similarly, for decisions that depend on the comparison of two nests' qualities, an ant is required to compare the quality of a candidate nest (with physical quality q_1 and population pop_1) and her home nest (with physical quality q_0 and population pop_0). We still use the sigmoidal function in Equation 2, with

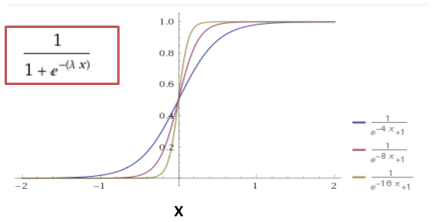


Figure 2: Sigmoidal function with $\lambda = 4, 8, 16$.

the change that the input x to the function now is

$$\frac{q_1 - q_0}{4} + \textbf{pop\_coeff} \times \frac{pop_1 - pop_0}{num\_ants} \tag{3}$$

where 4 is the maximum value of nest qualities, and num_ants is the total colony size.

Positive feedback through peer opinion is known to be important in collective intelligence generally, but has not been thoroughly explored in this system, beyond the quorum rule. The population effect we model here is thus a new way to consider the influence peer opinion in individual decision making during house hunting. It is different from quorum sensing since there is no threshold involved but instead a linear combination of population and physical attributes of the nest. The population effect hypothesis then states that the incorporation of population into nest quality assessments can offset the individual noise level represented by λ, and help with both the speed and consensus of emigration.

3 Model Parameters and Performance Metrics

In this section we describe all the parameters of our model. We also quantitatively define the speed and consensus measures for our predictions. A detailed description of the Python simulator implementation is in Appendix C, and the simulator code can be found online at

https://github.com/snowbabyjia/Collective-Decision-Making-HH.

3.1 Model Parameters

There are three kinds of parameters: environment, algorithm, and settings. In our Python simulator, these parameters are listed together in a configuration file. An example file is in Appendix C.

Environment parameters are controlled by the environment and not considered changeable or tunable. These include the number of ants in the colony, and the number and physical qualities of the nests as potential new nest options.

Algorithm parameters are parameters controlling probabilistic individual state transitions. These include λ for the sigmoid function in Equation 2, the pop_coeff value, parameters related to quorum sizes, the probability of finding a new nest in the environment, the probabilities of following and leading a FTR without getting lost, and the probability of continuing to transport instead of stopping transportation. More details are in B.1.2.

Settings parameters control plotting features and also convergence criteria. These include the option to generate a plot, the total number of runs for every environment/algorithm setting, the maximum number of rounds per simulation run, the percentage of ants needed in a nest to declare **convergence**, and the number of rounds the convergence needs to persist to declare **persistent convergence** which marks the end of the simulation run.

We note that our number of algorithm parameters, eight, is a significant decrease from those in the previous model (Table 1 in (Pratt et al. 2005)), thus making our model much more tractable and generalizable, as well as easier for collecting various statistics and adding extra features.

3.2 Default Parameter Values

The parameters values below are used as a default from Section 4 and 5, unless otherwise specified.

Algorithm Parameters Compared to the agent-based model in (Pratt et al. 2005), our model places less emphasis on assigning specific observed values to a large number of parameters, striving instead to be more agile in representing a wide range of possible behaviors. Some parameters have experimental "meanings" and can be estimated from empirical data, as shown in the next paragraph. Some parameters cannot be directly drawn from existing empirical data. We estimate these parameter values in a trial-and-error fashion. In general, the default values of these parameters are picked so that our simulation results match well with the empirical results in (Pratt et al. 2005) for one- and two-nest emigrations, as detailed in D.

The sources for determining the algorithm parameter values are listed in Table 1. In particular, the values of **lambda_sigmoid** (range: 1 to 16) and **pop_coeff** (range: 0 to 1) are picked by trial-and-error to model individual sensitivity to nest qualities, and the significance of colony information versus individual judgements. The quorum size (**quorum_thre** $\times$ (num_active+num_passive) + **quorum_offset**) is observed to have a median value between 4 and 18 ants for worker populations from 24 to 150, with the quorum size having a significant positive correlation with the number of adult ants (Pratt et al. 2002; Franks et al. 2015). Therefore, with a colony of 200 members (including 100 adult workers), we use a **quorum_thre** of 15% and set **quorum_offset** to 0, estimating a quorum size of 15. The value of **search_find** (range: 0 to 1) is determined experimentally by trial-and-error. This parameter can be influenced by many other factors such as the spatial geometry of the nests and the experience level of the individual. Although these nuances are not captured in our model in the

Parameter	Value	Source
lambda_sigmoid	8	trial-and-error, Sec. 4.1
pop_coeff	0.35	trial-and-error, Sec. 4.1
quorum_thre	0.15	(Pratt et al. 2002; Franks et al. 2015)
quorum_offset	0	(Pratt et al. 2002)
search_find	0.005	trial-and-error
follow_find	0.9	(Glaser et al. 2018; Pratt 2008)
lead_forward	0.6	trial-and-error
transport	0.7	(Pratt et al. 2005)

Table 1: Default parameter values and the sources that helped determine these values.

interest of simplicity, follow-up research (Cai et al. 2021) has already started extending our model to include these geospatial aspects. The parameter **follow_find** denotes the success rate of a tandem run without the follower getting lost and starting a new search. A successful tandem run requires that both ants reach the target nest. Empirical observations suggest large variation in tandem success, with observed success ranging from 30% to over 90% (Pratt 2008; Glaser et al. 2018). However, even lost followers enjoy a significantly increased chance of finding the target nest on their own (Pratt 2008). We thus chose a high FTR success rate of 0.9 to capture both these direct and indirect effects of tandem following on nest discovery. The parameter **lead_forward** (range: 0 to 1) is the probability that an ant performs an FTR when in the *lead_forward* state. The alternative option, *get_lost*, captures the fact that tandem leaders sometimes wander far from their target destination and thus have the opportunity to encounter other nest sites (i.e., they get lost and become searchers), and is determined experimentally in a trial-and-error fashion. The parameter **transport** is the probability that an ant keeps transporting instead of stopping to resume search for additional sites. The stopping probability is observed to be between 0.06 and 0.44, meaning our **transport** should take values between 0.56 and 0.94. We chose 0.7 as our baseline value.

Environment and Settings Parameters An average colony size of 200 with 50 active workers, 50 passive workers, and 100 brood items is within the range of real colony compositions (Franks et al. 2015). One round approximately translates to 0.5-1 minutes, though this is a very rough estimate. A simulation with 2000 rounds thus translates to 16-32 hours, and one with 4000 rounds translates to 32-64 hours. We set the default to 4000 to include some very slow emigrations observed in published reports (Pratt et al. 2006). The values for variables **percent_conv** and **persist_rounds** are determined by trial-and-error and rough estimates from past empirical observations.

3.3 Speed and Consensus Measures

Using the set of parameters that replicated the empirical data shown in (Pratt et al. 2005), we demonstrate the power of our model by testing new hypotheses and making new predictions as shown in Section 4. In order to do so, we define the speed and consensus performance metrics below for the *whole emigration process* until either convergence or the end of simulation, including cases resulting in splitting.

Convergence Score as Speed The final goal of the house hunting algorithm is to achieve fast convergence in any given environment and stabilize at that convergence. To assess how well this was achieved, we calculate a **convergence score** as the inverse of the round number when a persistent convergence started. If no persistent convergence was reached before the end of the simulation, the convergence score is 0. Each simulation run has a convergence score.

Consensus Another important metric is consensus, defined as the largest proportion of ants in any nest at the end of emigration. The end of an emigration is either when it reaches a persisted convergence, or when the simulation reaches

maximum number of rounds.

4 The Power of Population Effect

In this section, we explore the influence of the population effect on emigration speed and cohesion. We test the population effect hypothesis in an environment with two equal quality candidate nests, making it particularly challenging for colonies to reach consensus, or at least making it take much longer to do so. Section 4.1 explores correlations between **pop_coeff** and the degree of randomness in individual decision-making; and Section 4.2 reveals how **pop_coeff** decreases splitting by colonies facing two equal options.

4.1 Population Effect Helps with Emigration Speed

To investigate the influence of the population effect, we ran simulations for different combinations of **pop_coeff** (ranging from 0.002 to 0.8) and **lambda_sigmoid** (ranging from 2 to 16). We ran simulations for an environment containing two identical new nests [0,1,1]. For each combination of **pop_coeff** and **lambda_sigmoid**, we ran 500 simulations with a colony of size 200, consisting of 50 active workers, 50 passive workers, and 100 brood items.

Results The results show evidence for an inverse relation between **pop_coeff** and **lambda_sigmoid** (Fig. 3). For each value of **lambda_sigmoid** in the range [2,16], there is a value of **pop_coeff** that maximizes the convergence score, and this value increases as **lambda_sigmoid** decreases. Thus, when an individual ant makes noisy local decisions (modeled with lower values of **lambda_sigmoid**), she can counteract this deficiency by relying more on the input of her peers through a higher value of **pop_coeff**. We notice that as **lambda_sigmoid** increases, the optimal **pop_coeff** decreases, meaning that

individuals do not have to rely as much on peer opinions.

To gain further understanding of the optimal **pop_coeff** value for a colony, below we interpret the advantages and disadvantages of *increasing* the value of **pop_coeff**:

Advantages

- Higher momentum in the system. This can promote the colony to accumulate population at a certain nest more quickly, and thus achieve faster convergence.

- Better prevention of splits. Multiple candidate nests may reach the quorum, especially when the nests have similar physical qualities. This can lead to the colony splitting between more than one site. Population Effect via **pop_coeff** might help to break ties, by amplifying small random differences in the populations of competing sites.

Disadvantages

- Slower error correction. Since we are dealing with a randomized algorithm, there is always a chance that the colony will collectively make a "bad" temporary decision, even if individuals have low noise levels. The higher momentum will then make the wrong decision more "sticky" by accumulating more ants at a mediocre nest even if a better one is available. The colony would then have to move later to the better nest, adding costs in time and risk. In this way, high **pop_coeff** can cause slower convergence, and lead to "madness of the crowd".

These trade-offs suggest that there is an optimal value of **pop_coeff** for a given **lambda_sigmoid** as seen in Fig. 3. This predicts that colonies may

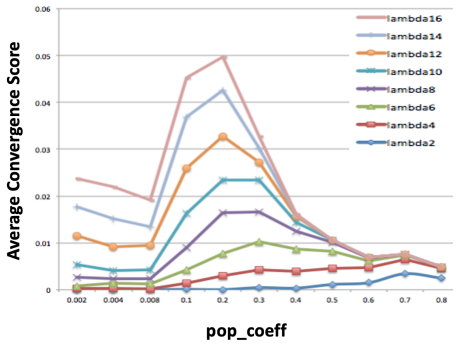


Figure 3: Average convergence score (across 500 simulations) as a function of **pop_coeff**. Different colored curves represent different **lambda_sigmoid** values as described in the individual decision model (Fig. 2). This shows that the optimal value of **pop_coeff** increases as **lambda_sigmoid** decreases.

tune **pop_coeff** according to the uncertainty of individual behavior in order to achieve the highest convergence score for a given environment.

4.2 Population Effect Helps with Consensus

In this section we further explore how a population effect can help colonies to reach consensus when faced with two identical nests. We explore this question by simulating emigrations in which a colony is presented with two identical nest sites. We assess how well they reach consensus on a single one. We also vary the degree of scout sensitivity to site population by considering different values of **pop_coeff**.

We ran 200 simulations each for **pop_coeff** = [0, 0.2, 0.4], in an environment with **nest_qualities** = [0,1,1]. We set **lambda_sigmoid** to 16 in order to be more sensitive to temporal differences in nest populations. We set the max number of simulation rounds to be 1000, equivalent to 8-16 hours empirically. After round 1000, emigrations may or may not reach consensus eventually, but in order to do controlled experiments to see the effects of different values of **pop_coeff** we enforce that all simulations have the same value of **num_rounds**,

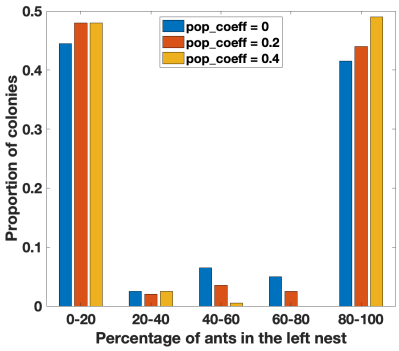


Figure 4: Simulation results for colonies choosing between two identical nests. The histograms show the distribution of the percentage of the colony occupying the left nest, for three different values of **pop_coeff**.

1000. The rest of the parameters take the default values.

Results The simulation results show strong symmetry breaking (Fig. 4). That is, a large majority of simulations ended with 80% to 100% of the colony in one of the two nests. When consensus was reached, it was roughly equally likely to be in nest 1 or nest 2, producing the distinctive U-shaped distribution seen in Fig. 4. This pattern was true regardless of the value of **pop_coeff**, suggesting that the quorum rule already generates strong symmetry breaking in this case. However, as the value of **pop_coeff** increases, the histograms also aggregate more towards the two end bins, meaning there are fewer split cases. Thus we confirm the positive effect of **pop_coeff** in reducing splits, either by prevention or by facilitating later re-unification. These mechanisms can have significant effects in more challenging environments with more candidate nests.

5 Other Predictions with Experimental Support

In this section we test other hypotheses concerning more complex scenarios where the link between colony patterns and individual behavior has not pre-

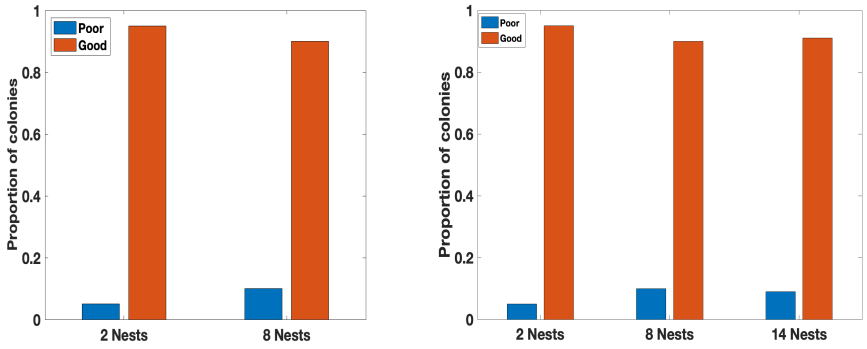
viously been modeled. For scenarios that have been explored empirically, we determine how well our model can account for observed results, and whether the empirical observations are comprehensive. Section 5.1 examines a colony's ability to choose well when faced with larger option arrays; and Section 5.2 focuses on how colonies make rational decision time investments depending on nest quality differences.

5.1 Colonies Have High Cognitive Capacity

How well do colonies perform when selecting from many nests? A previous study (Sasaki et al. 2012) showed that colonies are quite good at selecting a single good nest from a set of eight nests, four of which are good and four of which are mediocre. This is in contrast to individual ants, who are as likely to choose a mediocre as a good nest when faced with the same scenario. The colony advantage has been hypothesized to result from sharing the burden of nest assessment: very few of the scouts ever visit more than one or two nests, whereas a lone ant visits several, potentially overwhelming her ability to process information about them successfully (cognitive overload). We simulate this experiment to determine whether we can reproduce both the colony's ability and the observed distribution of nest visits across scouts.

We designed a simulated experiment with multiple nests in the environment, half of which are mediocre (physical_quality 1.0) and the rest of which are good (physical_quality 2.0). We considered three environments with 2, 8, and 14 nests, respectively. For each environment, We ran 600 simulations with a fixed colony size 200, containing 50 active and passive ants each, and 100 brood items.

Results First, we found that simulated colonies reached consensus on a good nest with high probability, matching that seen in empirical data (Fig. 5). This was true even when the number of nests was increased to 14.



(a) (b)

Figure 5: The proportions of colonies that eventually moved into poor or good nests. (a): Empirical results in 2-nest and 8-nest settings (Sasaki et al. 2012). (b): Simulation results from our model in 2-nest, 8-nest, and 14 nest settings.

Next, we verified that the high cognitive capacity of colonies is associated with a low number of nests visited by each scout. The proportion of ants visiting only one or two nest was similar in the simulations and experiments (Sasaki et al. 2012): over 80% of individual ants visited only one or two nests in the course of the emigration. Fig. 6 shows similar pattern is seen for the number of transports: that is, if we focus only on the ants who contributed to the emigration by transporting nestmates, over 80% visited only one or two nests. Ants that access many nests are few and have a minor role in the transportation process. Thus, colonies are less vulnerable to cognitive overloading compared to single ants when choosing among multiple sites, providing a possible explanation to the higher cognitive capacity of colonies.

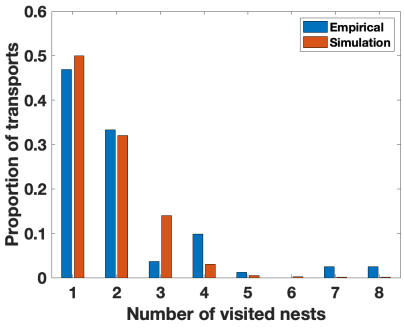


Figure 6: Proportions of transport efforts as a function of the number of candidate sites visited by each ant. The blue bars show the percentage of transports done by ants that visited a given number of nests (Sasaki et al. 2012), and the dark orange bars show the same for simulated ants. Colonies choose among eight nests (four good and four mediocre) in both simulations and experiments (Sasaki et al. 2012).

5.2 Colonies Make Rational Choices about Decision Speed

For choices between two nests, how does the difference between the nests affect the speed of decision-making? Counter-intuitively, a previous study (Sasaki et al. 2019) found that colonies move more quickly when site qualities are more similar. But this behavior accords with decision theory predictions that decision-makers should take less time if the consequences of their choice are small; that is, since the nests are similar in quality, the opportunity cost of making a wrong decision is small, so it's rational to save time costs by taking on a higher risk of choosing the wrong nest.

We simulate this scenario to determine if we can reproduce the same pattern, but we also explore a broader range of quality differences to better describe the relation between quality difference and decision time. We designed an environment with two candidate nests, one good and the other mediocre. The good nest has physical_quality 2 in all simulations, but the physical_quality of the mediocre nest varies across simulations from 0.2 to 1.7. We asked whether the

quality of the mediocre nest is correlated with the convergence score (a measure of decision speed). We ran 300 simulations for each environment with a colony of size 200, consisting of 50 active workers, 50 passive workers, and 100 brood items. We repeated this set of simulations for five different values of **lambda_sigmoid** values: [8,10,12,14,16].

Results If our model reproduces the rational time investment choices of colonies (Sasaki et al. 2019), then we expect the convergence score to increase as the mediocre nest quality increases, thus becoming more similar to the good nest. Our results partially match this prediction, with convergence score increasing as the mediocre nest quality goes from 0.2 to about 1 (Fig. 7). However, at higher mediocre nest qualities, the pattern reverses and convergence score declines. This basic pattern is seen for all tested values of **lambda_sigmoid**.

We propose that the nest qualities studied in (Sasaki et al. 2019) came from the region below the peak score that saw an increase of speed with decreasing quality difference. But from our more granular simulations, we predict that as the quality difference gets still smaller, the convergence score will start decreasing, meaning colonies will start investing more time.

Why might this happen? Recent studies have explained the behavioral difference between individuals and colonies via two different decision models: the tug-of-war model describes individual behavior, while colony behavior is better accounted for by the horse race model (Kacelnik et al. 2011). The tug-of-war correctly predicts the irrational behavior of individual ants, in that their decision-making slows down for options that are more similar. The horse race, in contrast, correctly predicts colonies' rational acceleration of decision making for similar options. We hypothesize that the applicability of these models to the colony's behavior changes as the quality difference changes. More specifically in Fig. 7, before the peak score is reached, the colony may effectively distribute its

decision-making across many ants with limited information, the situation envisioned in the horse-race model. After the peak score is reached, the colony may come to depend more on individual comparisons between nest sites made by a few well-informed ants, and thus to show the irrational slow-down predicted by the tug-of-war model. It could also be the case that more transports are performed between the two candidate nests as the likelihood of the mediocre nest achieving quorum attainment increases.

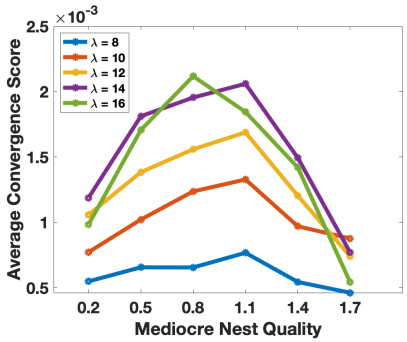


Figure 7: Average convergence score as a function of the physical_quality of the mediocre nest. The physical_quality of the good nest is 2, and that of the home nest is 0.

6 Discussion

In this paper, we developed a tractable agent-based model to examine the collective nest site selection process in colonies of *Temnothorax* ants. To test against existing experimental data and to make predictions, we built a convenient Python simulator that can easily be extended to add extra features. The model successfully replicated published individual and colony-level outcomes, and performed as well as an earlier model (Pratt et al. 2005) in accounting for underlying individual and colony behavior in one- and two-nest emigrations, but did so with a more concise set of individual decision rules. Using the set of pa-

rameter values that achieved the above, our model confirms a novel population effect hypothesis, which states that the integration of peer opinion, represented by a nest's population, is helpful for both the speed (Fig. 3) and consensus (Fig. 4) of emigrations.

On top of matching previous studies of simple one- and two- choice environments, our model also generated simulated results that confirmed emigration behavior in more realistic and challenging multi-nest environments that had not been modeled previously. Specifically, in Fig. 5 and 6 we show evidence that colonies, compared to single ants, make more accurate decisions among multiple nests because the former are minimally exposed to cognitive overloading, as shown experimentally in Sasaki et al. 2012. In addition, with partial empirical support, our model makes predictions on the quantitative relationships between emigration speed and the mediocre nest quality in a two-nest environment with one good and one inferior nest (Fig. 7). From these examples, we showed that the model and the accompanying software are versatile and easy to extend to additional investigations on unexplored scenarios such as emigrations in a changing environment. Moreover, the generalizable modeling framework that we introduced can be used to formally represent a variety of distributed algorithms used by animal groups to understand the emergence of collective intelligence in biological systems.

Although the presence of the population effect has not yet been shown in *Temnothorax* colonies, there is reason to expect that they would benefit from a behavioral rule to enhance consensus. They differ from other social insect species that achieve consensus through highly nonlinear recruitment mechanisms. For example, ant species that recruit via trail pheromones will choose one of two identical food sources rather than forming trails to both. This is because the attractiveness of a trail is a sigmoidal function of the amount of pheromone it

contains, which leads to rapid amplification of small random differences in the strengths of competing trails (Beckers et al. 1990; Perna et al. 2012). However, similar experiments on *Temnothorax* ants found that they do not always break symmetry, instead exploiting both feeders equally, a result that has been attributed to the linear relationship between tandem running effort and recruitment success (Shaffer et al. 2013). An open question is whether this lack of symmetry breaking also holds for nest site selection. When presented with identical nests, do colonies choose only one or split between them? If they can reach consensus, then how do they do so? One possibility is that the quorum rule provides sufficient non-linearity to amplify small random differences in site population, thus ensuring that the colony does not split. Another possibility is that colonies have some other mechanism of avoiding splits. A good candidate for such a mechanism is population effect explored in this paper. This would allow amplification of early random differences in population, by increasing the likelihood of recruitment to the nest with more ants. Further study is warranted to test whether this effect is found in real colonies.

In the rest of this section, we discuss several specific directions for future research. While our model captures many aspects of individual behavior, it leaves out some important features, including many that affect timing. These include 1) effects of the spatial distribution of nests, which is the focus of a recent modeling and data analysis study that extended our house-hunting model (Cai et al. 2021) has also demonstrated the value of this framework and the ease of use of our simulator, 2) effects of individual experience on recruitment probability and speed, and 3) actions that may last a variable duration such as the evaluation of a new nest. Adding these to the model would allow it to explore a broader range of colony abilities and to reveal as yet unknown components of individual behavior and how they interact with known aspects. For example,

more realistic models of timing would undoubtedly affect the discovery behavior currently captured by the single variable *search_find*.

On the simulation data analysis side, there are many directions for further research. First, we note the link between the effects of different quorum sizes and the horse-race and tug-of-war models that have been successfully used to describe group and individual decision-making, respectively, in these ants (Kacelnik et al. 2011). Our model finds that group decision-making may be better captured by the tug-of-war model when a colony is choosing between two very similar options. If so, this suggests that colonies can change their relative reliance on individual decision-making according to the decision context. This indicates the value of developing a more quantitative model that combines the tug-of-war and the horse-race models, based on the same factors that affect how a colony chooses the most beneficial quorum size.

Additionally, our model shows the potential utility of individual ants taking account of site population when assessing a site's quality. Whether real ants use peer opinions in this way has not yet been experimentally tested. Our results suggest that it may be important for preventing and repairing split decisions. However, the amount of peer opinions that individuals should rely on is an intricate balance, as we described in Section 4.1. It would be highly valuable to quantify the relationship between the frequency and degree of splitting to the quorum size and to **pop_coeff**. A related research direction is to find out other factors that allow colonies to robustly reunify in split cases. However, the runtime of our program over hundreds of simulations can be significant, making it difficult to investigate the system dynamics and performance in all possible parameter settings. Overcoming this challenge requires software optimization techniques such as code parallelization and possibly further model simplifications.

On the theoretical analysis side, our model serves as a stepping stone for more rigorous mathematical formulations and proofs of guaranteed bounds on any metrics of interest. Starting with simpler environments, our model can be reduced to analytically derive the goals different mechanisms can and cannot achieve. These results can then potentially provide insights on why certain collective behaviors have emerged through evolution, as well as on engineering artificial distributed systems subject to similar limitations to reach consensus. In fact, a recent theoretical work on the effect of quorums in single-nest emigrations (Zhang et al. 2021) demonstrates the value of our house-hunting model.

Finally, we emphasize that our modeling framework can be flexibly adapted to other distributed algorithms inspired by animal groups. One compelling example is that honeybee colonies use a very similar algorithm in their nest-selection process (Laomettachit et al. 2016), and can be easily modeled by our framework. Comparing it to our ant colony model can reveal commonalities and differences in how different animal groups achieve various goals and organize potentially conflicting priorities.

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Author Disclosure Statement

The authors declare they have no competing financial interests.

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Appendix

A Modeling Framework

In this section, we introduce a general modeling "language" that has the potential to be useful for a wide range of applications. In B, we instantiate this language in the context of the house hunting process in ant colonies.

A.1 Agent-based Model

Formally, the components below define the entities in the system and their static capabilities. More explanatory text follows after the list.

- **agent-ids**, a set of ids for agents. Each *agent-id* uniquely identifies an agent. We also define **agent-ids**$'$ to be **agent-ids** $\cup\{\perp\}$ where $\perp$ is a placeholder for "no agent". In general, we add $'$ to a set name to denote the original set with the addition of a default element $\{\perp\}$.

- **external-states**, a set of external states an agent might be in. Each element in the set is an *external-state*. In addition, **all-externals** is the set of all mappings from **agent-ids** to **external-states**. Each element of the set is an *all-external*.

- **internal-states**, a set of internal states an agent might be in. Each element in the set is an *internal-state*.

- **env-states**, a set of states that the agents' environment might take on. Each element in the set is a *env-state*.

- **action-types**, a set of the types of actions agents might perform. Each element in the set is an *action-type*.

- **env-choices**, a set of values an agent can access in the environment. Each element in the set is an *env-choice*.

- **actions**, a set of quadruples of the form (*action-type, agent-id, agent-id′, env-choice*) $\in$ **action-types** $\times$ **agent-ids** $\times$ **agent-ids′** $\times$ **env-choices**. Each element in the set is an *action*.

- **select-action**(*agent-id, state, env-state, all-external*): A *state* is a pair of (*external-state, internal-state*) $\in$ **external-states** $\times$ **internal-states**. Each (*agent-id, state, env-state, all-external*) quadruple is mapped to a probability distribution over the sample space of **actions**, for which the second component is equal to the input argument *agent-id* and the third component is not equal to it. The function then outputs this probability distribution.

- **transition**(*agent-id, state, all-external, action*): A *state* is a pair of (*external-state, internal-state*) $\in$ **external-states** $\times$ **internal-states**. Each (*agent-id, state, all-external, action*) quadruple determines a *state* as the resulting state of the agent identified by the input argument *agent-id*. The function outputs the resulting *state*.

Each agent has a unique *agent-id* $\in$ **agent-ids**, and is modeled by a state machine. Agents can transition from one *state* to another. A *state* is a pair: an *external-state* $\in$ **external-states** that is visible to other agents, and an *internal-state* $\in$ **internal-states** that is invisible to other agents.

We define **all-externals** to be the set of all mappings from **agent-ids** to **external-states**. Each element of the set is an *all-external* and represents a particular mapping from **agent-ids** to **external-states** where each *agent-id* is mapped to an *external-state*.

The set **env-states** represents the set of states that the agents' environment

might take on. In this paper, we will assume that the environment is fixed. That is, the *env-state* does not change during the execution of the system. The reason we use a set here is to enable us to model the same set of agents operating in different environments.

Agents can also access values in the environment, and each value is called an *env-choice*. The set **env-choices** is the set of all possible values for *env-choice*.

An agent can transition from one *state* to another by taking an *action* $\in$ **actions**. Each *action* consists of an *action-type* $\in$ **action-types**, the id of the initiating agent *agent-id* $\in$ **agent-ids**, the id of the (optional) received agent *agent-id*$'$ $\in$ **agent-ids**$'$, and *env-choice* $\in$ **env-choices**.

The function **select-action**(*agent-id, state, env-state, all-external*) is intended to select an *action* for the agent with the given *agent-id*, who is the initiating agent in the *action*. The function outputs a probability distribution over the sample space **actions**. However the sample space limits its elements to have the second component equal to the input argument *agent-id*, and the third component not equal to it. Thus, any sampled *action* will have *agent-id* being the initiating agent's id, and the (optional) receiving agent necessarily has a different id.

The function **transition**(*agent-id, state, all-external, action*) represents a transition to be performed by the agent identified by the input argument *agent-id*. Given the input arguments, the function deterministically outputs the resulting *state* of the transition.

A.2 Timing and Execution Model

In this section, we introduce the dynamic aspects of our model, including the discrete and synchronous timing model, and how different components in the system interact with each other at different points during the execution of the

algorithm.

Our system configuration contains 1) an environment state, called *env-state*, and 2) each agent's *state*, which is a pair (*external-state, internal-state*), independent of *env-state*. Agents receive inputs from and react to the environment during the execution of the system. In this paper, we will assume that the environment is fixed. That is, the *env-state* does not change during the execution of the system.

Incorporating some theoretical ideas from (Ghaffari et al. 2015; Radeva 2017), we divide the total time into *rounds*. Each round is a discrete time-step, and times are the points between rounds. At any time t, there is a corresponding system configuration t. The initial time is time 0, and the first round is round 1, taking the system from configuration 0 at time 0 to configuration 1 at time 1. In general, round t starts with system configuration $(t-1)$. During round t, agents can perform various **transition**'s, which take the system from configuration $(t-1)$ at time $(t-1)$ to configuration t at time t.

We now describe the execution of an arbitrary round t. At any point in the execution of round t, each agent x is mapped to a *state*, *state_x*, which is visible to agent x itself. However, to other agents, only agent x's *external-state*, *external_x* is visible. We denote *all-external* $\in$ **all-externals** to be the mapping from every *agent-id* $\in$ **agent-ids** to the corresponding *external-state* $\in$ **external-states** in round t. These mappings can be updated during the execution.

Accounting for the randomness of the order of execution for all the agents, a randomly chosen permutation of **agent-ids** is generated at the beginning of round t, serving as the order of execution for the agents in the round. We also instantiate a set $Trans = \emptyset$ at the beginning of the round. An agent is prevented from changing its *state* further in the round once it adds its *agent-id* to $Trans$,

which can happen during its turn (even if there is no resulting state change) or when it performs a **transition** during another agent's turn. As a result, each agent can change its state at most once in the round. After all agents are in the set *Trans*, round t is over, and all agents enter round $t+1$ synchronously.

The rest of this section describes all possible operations during one agent x's turn in round t. When an agent with *agent-id* x (a.k.a. agent x) gets its turn to execute, it first checks whether $x \in Trans$. If so, agent x does nothing and ends its turn here.

Otherwise, agent x has not yet transitioned in round t. Let *state_x* denote the *state* of agent x. Agent x calls the function **select-action**(*x, state_x, env-state, all-external*). The function outputs a probability distribution over the sample space of a subspace of **actions**, for which the second component is x, and the third component is not x. Agent x randomly selects an *action*, $act = (a, x, x', e)$, according to this probability distribution.

Agent x then calls **transition**(*x, state_x, all-external, act*), to determine the resulting *state*, *new_state_x*, for agent x. As the initiating agent, x also gets added to $Trans$. Next, in the case where $x' \neq \perp$, agent x' also calls **transition**(x', *state_x', all-external, act*) where *state_x'* is the current *state* of agent x', maps itself to the function output, and updates its entry in *all-external*. Note that x' is added to $Trans$ if the function output is different than *state_x'* in any way. This is the end of agent x's **transition** call. Agent x then maps itself to the resulting state *new_state_x*, and updates its entry in *all-external*. Agent x finally ends its turn here.

A.3 Discussion

Although our model keeps track of the *external-state* of all the agents in *all-external*, when performing a transition, an agent can only access *local* informa-

tion in it. Locality here is flexible to the context, i.e. local to the location of the agent initiating an action.

Agent-based models are especially powerful for simulating and analyzing collective behaviors given their natural compatibility with object-oriented programming methodologies and their flexibility for allowing individual differences in realized state transition probabilities among the agents (De Vries et al. 1998; Sumpter et al. 2001; Masuda et al. 2015b; Pratt et al. 2005).

B House Hunting Model Details

B.1 Formal Model

B.1.1 Model components

In this section, we show how each component in our modeling framework (A.1) is defined in the house hunting algorithm context.

```
class Nest:
  float physical_quality

class Ant:
  AgentState cur_state
  Action proposed_action
  int ant_id # unique identifier

class AgentState:
  class ExternalState:
    char phase
    string state_name
    int role
    int location
  class  InternalState:
    int terminate_count
    int home_nest
    int candidate_nest
    int old_candidate_nest

class Action:
  string action_type
  int initiating
  int receiving = -1 # Invalid default value.
  int env-choice = -1 # Invalid default value.
```

Figure 8: Native data structures that define different entities in the distributed system.

Fig. 8 shows our native data structures as used by various components in the system: *Nest* objects, an array which constitutes an *env-state*; *Ant* objects, each corresponding to an agent; *State = (ExternalState, InternalState)* objects, each corresponding to a *state = (external-state, internal-state)*, and *Action* objects, each corresponding to an *action*. Each of the data structures contains a set of variables, as seen in Fig. 8. Note that we consider all variables belonging to either the class *ExternalState* or the class *InternalState* to belong to the class *State* as well. Throughout the rest of the paper, we use the notation *object.variable* to denote the value of a *variable* belonging to a class *object*. Using these data structures as building blocks, we now show all possible values for the components in the framework presented in A.1. Note that for consistency with our implementation in C, we use -1 or an empty string "" to represent any invalid default integer or string values represented by $\perp$ in A.

- **agent-ids**, the set containing all integers in the range [0, num_ants), where num_ants is the total number of ants in the colony. In addition, **agent-ids**$'$ = **agent-ids** $\cup$ -1. Each *Ant* is initialized with its corresponding *ant_id*, which corresponds to a *agent-id*.

- **external-states**, the set containing all possible values for an *External-State* class object, each corresponding to an *external-state*. We designed these variables to be in the *external-state* because these contain information that influences other ants' activities. Therefore, it is biologically plausible that individuals have access to this information about one another.

  In any *ExternalState* class object, *phase* has one of four possibilities - Exploration (searching for new nests), Assessment (assessing new nests), Canvassing (leading other active workers on FTRs to her accepted candidate nest), and Transport (committing to the new nest and rapidly car-

rying other ants to it). Note we abbreviate the four phases to names "E", "A", "C" and "T", respectively. The initialization of an *Ant*'s *phase* and *state_name* can be found in B.1.3. For each *phase*, the variable *state_name* take values from a different set, as follows:

```
E: at_nest, search, follow, arrive
A: at_nest, search, follow, arrive
C: at_nest, search, arrive, lead_forward, quorum_sensing
T: at_nest, search, follow, arrive, transport, reverse_lead
```

Figure 9: *state_name*'s available for each phase.

The variable *role* can be one of (0,1,2) representing (active ant, passive ant, brood), and each *Ant* is initialized with the appropriate value. The variable *location* can be any integer in the range [0, num_nests) where num_nests is the total number of nests in the environment, with 0 representing the original home nest. In addition, recall that **all-externals** is the set of all possible mappings from **agent-ids** to **external-states**. Each element of the set is an *all-external*.

- **internal-states**, the set containing all possible values for an *InternalState* class object, each corresponding to an *internal-state*. The set of fields we designed for the *InternalState* class represent information that should only be accessed and modified by an ant's internal memory. Each of *home_nest* (initial value = 0), *candidate_nest* (initial value = -1), and *old_candidate_nest* (initial value = -1) can take any integer in the range [0, num_nests), where num_nests is the total number of nests. Lastly, *terminate_count* (initial value = 0) takes any value in the range [0, 10].

- **env-states**, a set of arrays, each being an array of the *Nest* class objects. Each array corresponds to an *env-state*. For an *env-state*, the *Nest* at index 0 represents the original home nest and has *physical_quality* 0. All other *Nest*'s have *physical_quality* in range [0, 4]. The maximum quality

4 here is arbitrary. Recall that the array does not change throughout the execution of the system, and the array is read from a configuration file introduced in 3.1.

- **action-types**, the set of the types of actions includes: "search", "no_action", "find", "follow_find", "get_lost", "reject", "no_reject", "accept", "recruit", "quorum_met", "quorum_not_met", "stop_trans", "delay", "terminate", "lead", "carry". *Action-type* is initialized to "no_action". Each item in the set above is an *action-type*.

- **env-choices**, the set of integers in [0, num_nests) $\cup$ -1 where num_nests is the number of nests in the environment. Each element in the set is an *env-choice* and is an integer representing an index into *env-state*. An *env-choice* has initial value -1.

- **actions**, the same set as defined in A.1. Note that not all actions require a receiving agent, and not all actions require an *env-choice*. In case that they are not needed, they take the invalid default value -1.

- **select-action**(*agent-id, state, env-state, all-external*): the same function as defined in A.1. Refer to B.1.2 for details.

- **transition**(*agent-id, state, all-external, action*): the same function as defined in A.1. Refer to B.1.3 for details.

B.1.2 The select-action function

The function **select-action**(*x, state_x, env-state, all-external*) outputs a probability distribution over the sample space of **actions**, for which the second component is equal to the input argument *agent-id* and the third component is not equal to it. Let any *action* in the sample space be denoted by (a, x, x', ec),

where the second component is fixed. We now list out the probability distribution on other components for each possible value of the *state_name* variable in *state_x*, as it is the only variable in *state_x* that affects the output probability distribution. The boldface words are parameters that we can tune and whose values are read from a configuration file, introduced in 3.1.

- For *search*, the probabilities of choosing a to be "find" and "no_action" are **search_find** and 1-**search_find** respectively, and all other *action-type*'s have 0 probability. Both variables x' and *ec* take the invalid default value -1 with probability 1.

- For $follow$, the probabilities of choosing a to be "follow_find" and "get_lost" are **follow_find** and 1-**follow_find** respectively, and all other *action-type*'s have 0 probability. Both variables x' and *ec* take the invalid default value -1 with probability 1.

- For $reverse\_lead$, the probabilities of choosing a to be"delay" and "no_action" are **transport** and 1-**transport** respectively, and all other *action-type*'s have 0 probability. Both variables x' and *ec* take the invalid default value -1 with probability 1.

- For *quorum_sensing*, let the set $\tilde{X}$ be the set containing id's of all agents with *external-state* having $role \in \{0, 1\}$ and $location = state\_x.location$. If the set size $|\tilde{X}| \geq$ **quorum_threshold**, the probabilities of choosing a to be "quorum_met" and "quorum_not_met" are 1 and 0 respectively, and are 0 and 1 otherwise, and all other *action-type*'s have 0 probability. Both variables x' and *ec* take the invalid default value -1 with probability 1.

- For $lead\_forward$, let $\tilde{X}$ be the set containing id's of the agents that are not x, and whose *external-state* has $role = 0$ and $location = state\_x.location$.

The function selects an action $\widetilde{act} = (\tilde{a}, x, x', ec)$ according to the following probability distribution. In case *terminate_count* < 10, $\tilde{a}$ is chosen among "lead" and "get_lost" with probabilities **lead_forward** and 1-**lead_forward** respectively, and all other *action-type*'s have probability 0. In case *terminate_count* ≥ 10, $\tilde{a}$ is "terminate" with probability 1. The variable ec is equal to $\{state\_x.candidate\_nest\}$ with probability 1. The distribution of x' depends on $\tilde{a}$, as follows:

  - For "lead", if $\tilde{X} \neq \emptyset$, the variable x' is uniformly selected from $\tilde{X}$, and all other values in *agent-id*$'$ have 0 probability; otherwise, $x' = -1$ with probability 1.
  - For "get_lost", $x' = -1$ with probability 1.
  - For "terminate", $x' = -1$ with probability 1.

- For *transport*, let $\tilde{X}$ be the set containing id's of all agents that are not x, and whose *external-state* has *location* $=$ *state_x.location*. In addition, let $\tilde{X}'$ be the subset of $\tilde{X}$ containing agents that have *role* $\in \{1, 2\}$. The function first selects an action $\widetilde{act} = (\tilde{a}, x, x', ec)$ according to the following probability distribution. In case *terminate_count* < 10, $\tilde{a}$ is chosen among "carry" and "stop_trans" with probabilities **transport** and 1-**transport** respectively, and all other *action-type*s have probability 0. In case *terminate_count* ≥ 10, $\tilde{a}$ is "terminate" with probability 1. The variable ec is equal to $\{state\_x.home\_nest\}$ with probability 1. The distribution of x' depends on $\tilde{a}$, as follows:

  - For "carry", if $\tilde{X}' \neq \emptyset$, x' is uniformly sampled from $\tilde{X}'$, and all other values in *agent-id*$'$ have 0 probability. Otherwise if $\tilde{X}' = \emptyset \cap \tilde{X} \neq \emptyset$, x' is uniformly sampled from $\tilde{X}$, and all other values in *agent-id*$'$ have 0 probability. Otherwise, $x' = -1$ with probability 1.

  - For "stop_trans", $x' = -1$ with probability 1.
  - For "terminate", $x' = -1$ with probability 1.

- For *at_nest*, the probability of choosing a to be "search" is $1-p(x)$, where x is the quality of the nest option under assessment (Figure. 1) and $p(x)$ defined in Equation 2. There are always two possible actions for a *state* with $state\_name = at\_nest$, and the one that is not "search" naturally has probability $p(x)$ (Eq. 2). All other *action-type*'s have 0 probability. Both variables x' and ec take the invalid default value -1 with probability 1.

- For *arrive*, the probabilities of choosing a to be "reject" and "no_reject" are $1 - p(x)$ and $p(x)$ respectively, where x is the difference in quality of the candidate nest compared to the home nest (Eq. 3) and $p(x)$ defined in Equation 2. All other *action-type*'s have 0 probability. The variable x' take the invalid default value -1 with probability 1. The variable ec take the invalid default value -1 with probability 1.

B.1.3 The transition function

Passive Workers and Brood Items Active worker scouts are defined as those who engage in the emigration process by independently discovering the new nests (entering without carrying or being carried) or by carrying brood items or other adult ants to the new nest or both. Passive workers remain in the old nest until they are carried to the new nest. Brood items are similar to passive workers but do not contribute to quorum attainment (Pratt et al. 2002; Dornhaus et al. 2008).

We use sn_p to denote a *state* with a certain $state\_name = sn$ and $phase = p$. Passive workers and brood items together form the passive majority population in the colony. Their behavior pattern is thus very simple — they only have one $state\_name_{phase}$, at_nest_E, available to them. They can only allow one *action*

with *action-type* "carry" and themselves as the receiving agent. The action results in the *location* variable in their *state* set to the last component of the action, *env-choice*, and no other variables in their *state*'s can change throughout the execution. Therefore, the rest of the section focus on the *state* transitions of **active** workers only, including any initiating and receiving ants involved.

Initiation and Termination of Emigration All ants start in at_nest_E. Their *role* variable values are assigned the corresponding numbers, and *home_nest*, *location* are both initiated with 0, the original home nest. The variables *candidate_nest* and *old_candidate_nest* are set to -1 as the default invalid value. And *terminate_count* starts with 0.

We do not designate a separate "termination state" that disables an ant from exploring further, but at the termination of the emigration process, we expect most active workers to be in at_nest_E. This is enforced softly through the population effect introduced in B.1.2 - if an agent in at_nest_E is in a nest with both a high physical quality and a high nest population it is highly likely that she is happy staying put in this nest and stabilizes in the state at_nest_E. As a result, the more agents stabilizes in the same nest, the more likely that they will stay stable and that new agents will stabilize as well. In the house hunting algorithm, the conditions that trigger this "termination" behavior contains two cases, as mentioned in Section 2.1. The details of this special "termination" case handling is discussed in the next paragraph.

Special and General Cases In the house-hunting algorithm, there are some special cases that the **transition** function handles before outputting the resulting *state*. To facilitate, we define a set **allowed-in**(*external-state*) to be a mapping from **external-states** to subsets of **action-types**. Consider an *external-state* s, and the allowed subset is then **allowed-in**(s), representing the

set of actions the agent in the *external-state* s is allowed to receive. The four variables s contains (as shown in the *ExternalState* class) each affects **allowed-in**(s) in the following way. *location* has no influence. If *role* is 1 (passive) or 2 (brood), **allowed-in**(s) = "carry". Otherwise, $role = 0$. Let $state\_name_{phase}$ denote the *state_name* and *phase* variables in s. For at_nest_E, at_nest_A, and at_nest_T, **allowed-in**(s) = "lead", "carry". For $search_E$, $search_A$, $search_C$, $search_T$, and at_nest_C, **allowed-in**(s) = "carry". For all other cases, **allowed-in**(s) = $\emptyset$.

We now list out how the function **transition**(*agent-id, state, all-external, action*) handles each of the special cases, and also the general case. Let the input argument *action* be expanded to the quadruple ($act = a$, x, x', ec). Also recall that the set $Trans$ is a set containing the id's of all the agents that have completed a *state* change in the round (Section A.2).

- The first special case is if the input argument *agent-id* $= x'$. This case only happens when agent $x' \neq -1$ invokes (in agent x's turn) a **transition**(x', *state, all-external, act*), where $state = (external', internal')$ is the current *state* of agent x'. If $x' \in Trans$ or if $a \notin$ **allowed-in**($external'$), the function simply ends by returning the input argument *state*. Otherwise, the function adds x' to $Trans$. It then finds the black text box corresponding to *state.phase* and *state.state_name* in Fig. 1a, and the black text box that a leads to contains the *phase* and *state_name* of the resulting *state*. The rest of the variables in *state* are modified as well, and the details are listed for each possible value of the (*phase*, *state_name*) pair at the end of the section. The function then outputs the resulting *state*.

- The second special case is if *act* satisfies the termination condition mentioned earlier in this Section. Specifically, the cases are when *agent-id* $= x$, and *act* is either 1) $(lead\_forward, x, x', state\_x.candidate\_nest)$ and

$x' \neq -1$ has an *external-state* with $state\_name = lead\_forward$, or 2) $(transport, x, x', state\_x.home\_nest)$ and $x' \neq -1$ has an *external-state* with $state\_name = transport$. We call these the "termination conditions". When *act* satisfied either clauses, after adding x to $Trans$, the function ends its execution by outputting a resulting *state* that only differs from the input argument *state* by adding 1 to the *terminate_count* variable.

- The third special case is if *agent-id* $= x$ and *act* does not satisfy the termination conditions, but $x' \neq -1$ and either of the following is true: 1) $x' \in Trans$, or 2) $a \notin$ **allowed-in**$(external')$. Note the second case here excludes cases that satisfy our termination conditions stated in the last bullet point. In other words, the second special case has priority over this third special case. In this third special case, the function adds x to $Trans$, and ends its execution by outputting the original input argument, *state*.

- Lastly, in the general case where none of the above special cases applies, the function first adds x to $Trans$. Then it finds the black text box corresponding to *state.phase* and *state.state_name* in Fig. 1b, and the black text box that a leads to contains the *phase* and *state_name* of the resulting *state*. The rest of the variables in *state* are modified as well. The rest of this sections lists details for each possible value of the (*phase*, *state_name*), as described in Fig. 1. The function then outputs the resulting *state*.

In Fig. 1a and Fig. 1b, *action-type*'s are color-coded as shown in Table 2. We walk through all possible transitions of an ant and the associated changes in the internal and external states, in a phase-by-phase fashion.

Exploration

Arrow Color	Init/Recv	Phase Change
blue	Initiating	No
red	Initiating	Yes
purple	Receiving	No
green	Receiving	Yes

Table 2: Color coding of arrows representing *action-type*'s in Fig. 1a and Fig. 1b.

- An ant in at_nest_E has four possible actions. First, she can perform "no_action" and remain in the current nest. Second, she can perform "search" and go into the state $search_E$. Third, she can receive a "lead" by another ant to follow a FTR to a destination nest, $ec \in$ **env-choices**, in which case she sets *old_candidate_nest* to the value of *candidate_nest*, and sets *candidate_nest* to *ec*. Then she transitions to the state $follow_E$. Finally, she can receive a "carry" by another active worker ant to a destination nest $ec \in$ **env-choices**, in which case her *location* and *candidate_nest* are changed to *ec*, and she stays in at_nest_E.

- An ant is in the state $follow_E$ if she is in the middle of following an FTR, and has two possible actions. First, she can successfully follow the FTR to the destination nest ("follow_find") and change her *location* to her *candidate_nest*, which results in the state $arrive_E$. Otherwise, she may lose contact with her tandem leader ("get_lost"), and then enters the state $search_E$ and assigns the value of *old_candidate_nest* to *candidate_nest*.

- An ant in the state $search_E$ has three possible actions. First, she can have "no_action" and transition to at_nest_E by staying at her last known *location*. Second, she can "find" a new nest, $ec \in$ **env-choices**, in this round, assign the value of *candidate_nest* to *old_candidate_nest* and assign *ec* to both *location* and *candidate_nest*, and transition into $arrive_E$ state to evaluate it further. Third, she can receive an action, "carry", and the

results are the same as receiving the "carry" action in at_nest_E.

- An ant in the state $arrive_E$ has two action options. First, she can "reject" the nest she just arrived at. She then assigns the value of *candidate_nest* to *location* and then that of *old_candidate_nest* to *candidate_nest* go into the $search_E$ state. Otherwise, if she performs "no_reject", she transitions into the state at_nest_A and assigns the value of *candidate_nest* to *location*.

Assessment

- An ant in the state at_nest_A is assessing a new nest and is currently located at that nest. From here, three actions are available. First, she can "accept" the nest if she deems it high quality, which results in her transitioning to at_nest_C. Second, she may perform "search" to get into the $search_A$ state. Third, she can receive a "lead" by another ant to follow a FTR to a destination nest, in which case she assigns the value of *candidate_nest* to *old_candidate_nest* and assigns the destination nest $ec \in$ **env-choices** to *candidate_nest*, and then she transitions to the state $follow_A$. Finally, she can receive a "carry" by another active worker ant to a destination nest $ec \in$ **env-choices**, in which case her *location* and *candidate_nest* are changed to ec and transitions back to at_nest_E.

- An ant in the states $follow_A$ or $search_A$ has the same options and variable changes as in $follow_E$ or $search_E$ respectively, but the resulting state subscripted with A except the "carry" action.

- An ant in $arrive_A$ state has the same options and variable changes as in $arrive_E$, but with "reject" action leading to $search_C$.

Canvassing

- An ant in at_nest_C state has three available actions. First, she can decide to "recruit" and go into $quorum\_sensing_C$ state. Second, she can decide to "search" more and result in $search_C$ state. Third, she may receive a "carry" by another active worker ant to a destination nest, in which case her *location* and *candidate_nest* are changed to that nest and results back to at_nest_E.

- An ant in $quorum\_sensing_C$ state is at a nest different than her home nest, and has two options. If she estimates the current nest population to be higher than the quorum threshold, she performs "quorum_met", swap the values of *home_nest* and *candidate_nest*, and enters the state $transport_T$. Otherwise, she performs "quorum_not_met" and enters $lead\_forward_C$ state.

- An ant in $lead\_forward_C$ state has three actions available to her. First, she can "lead" another active worker and lead her on an FTR from the original home nest to the candidate new nest. She changes her *location* to the value of *candidate_nest*, and enters at_nest_C state. Second, she can "get_lost" in the process if she loses contact with the follower, and enters $search_C$ state. Lastly, she can "terminate" her emigration if the termination conditions are met, namely if she has repeated attempts to call other active workers who are also in $lead\_forward_C$ state. In this case, she changes her *location* to her *home_nest*, resets *terminate_count* to 0, and enters state at_nest_E.

- An ant in $search_C$ state has the same options and variable changes as in $search_E$ with the resulting state sub-scripted with C.

- An ant in $arrive_C$ state has the same options and variable changes as in $arrive_E$, but with "reject" action leading to $search_C$.

Transport

- An ant in at_nest_T state has the same options and variable changes as in at_nest_C with the resulting state sub-scripted with T, except that a "recruit" action results in $transport_T$, and that it can receive one additional action "lead", in which case she assigns the value of *candidate_nest* to *old_candidate_nest*, assigns the destination nest $ec \in$ **env-choices** to *candidate_nest*, and transitions to $follow_T$.

- An ant in $transport_T$ state has three available actions. First, she can decide to carry another ant, active, passive, or brood, to her newly committed nest. This results in her entering $reverse\_lead_T$ mode, meaning she can lead a reverse tandem run (RTR). These are tandem runs lead from the newly committed nest to the old home nest or another nest. Second, she can decide to "stop_trans" and stops her transport to go into the state $search_T$. Third, similar to the state $lead\_forward_C$, there is a "terminate" action when the termination condition is met, namely if she has repeated attempts to carry other active workers who are also in $transport_T$ state. In this case, she changes her *location* to her *home_nest*, resets *terminate_count* to 0, and enters state at_nest_E.

- An ant in $reverse\_lead_T$ only has two actions as her options. First, she may perform *no_action* and returns to at_nest_T state. Second, she may experience "delay" in her tandem runs, and will stay in $reverse\_lead_T$ state. There's no conclusion on the purpose of RTRs at this point in the research community, so we model it as a round-trip from an agent's candidate nest to the original home nest and back, eventually ending up with no state changes.

- An ant in the states $follow_T$ or $search_T$ has the same options and variable

changes as in $follow_E$ or $search_E$ respectively, but the resulting state are sub-scripted with T except the "carry" action.

- An ant in $arrive_T$ state has the same options and variable changes as in $arrive_A$, but with "reject" action leading to $transport_T$.

C Simulation Details

The Python code for the simulator can be found at:
https://github.com/snowbabyjia/Collective-Decision-Making-HH.

C.1 Sample Configuration File

```
[ENVIRONMENT]
num_ants = 200
nest_qualities = 0,1,2

[ALGO]
lambda_sigmoid = 8
pop_coeff = 0.35
quorum_thre = 0.15
quorum_offset = 0
search_find = 0.005
follow_find = 0.9
lead_forward = 0.6
transport = 0.7

[SETTINGS]
plot = 0
total_runs_per_setup = 500
num_rounds = 4000
percent_conv = 0.9
persist_rounds = 200
```

C.2 Data Structures and Global Variables

We define four native data structures, as shown in Fig. 8. The global variables include 1) the transition tables defined in Fig. 1, 2) *Nests*, the array of all nests including the home nest which by default has quality 0 and id 0, and 3) *Ants*, the array of all ants in the colony.

C.3 Simulation Overview

We describe our algorithm implementation in details below. Our executable software and instructions are available upon request.

Consider a colony of size num_ants where all the ants start the house-hunting task synchronously. We divide the total time to completion into $rounds$, with a maximum round number of $total\_runs\_per\_setup$.

At the beginning of round t, no ant has transitioned yet (instantiate *Trans* $= \emptyset$). Then a random permutation of all ant_ids is generated as the order of execution. When an ant gets her turn during this round, she first checks if her ant_id is in *Trans*. If so, she does nothing. Otherwise, knowing its id and current state, she chooses an action for this round according to the probability distribution defined in the **select-action** function.

The action picked by an ant x has an $action\_type$, a receiving ant id, and a nest id. Please note here that in real ant colonies, an action can involve either just a single ant, or a pair of ants (tandem run and carry). In the single ant action case, the receiving ant's id is assigned value -1. In the pair ant action case, the action includes the valid ant_id of the receiving ant y. Similarly, not all actions require a nest, in which case the nest id for the action is -1.

By looking up the *Ants* array, x can also get the current external state of all ants including the receiving ant y, if any, of the picked action. These values are enough for x to call the **transition** function, and adds its own id to *Trans*. The special case handling is detailed in Section 2.2.3 in the main manuscript, including the case where y might also call a **transition** function and adds itself to *Trans*.

When one round finishes, each ant has had one chance to initiate or receive an action, and potentially has a new state. Repeat rounds like the above until the criteria is met for convergence with persistence, or until the program reaches

the maximum number of rounds specified in the configuration file.

D Parameter Estimation

We estimate the various parameters in our model using the same empirical dataset that were successfully accounted for by an earlier model (Pratt et al. 2005) for emigrations in simple one- and two-new-nest environments.

Just like the parameter estimation technique used in (Pratt et al. 2005), we first examine a simple scenario where colonies have only one candidate nest in the environment. Then we consider a decision between two nests that clearly differ in quality. For all scenarios, we compare our simulation results to the same empirical data collected by (Pratt et al. 2005), at both individual and colony level. All simulations for the rest of the paper default to the default values described in Section 3.1, unless specified otherwise.

D.1 Single-Nest Emigrations

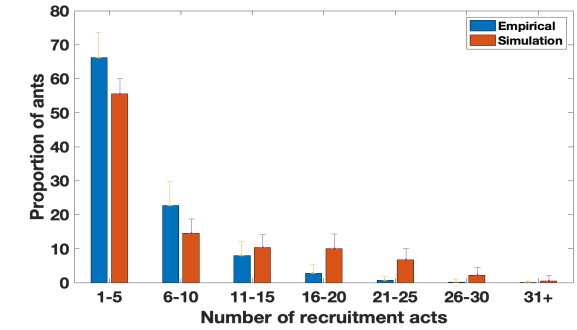
The first question we ask is: does our model accurately reproduce statistics on individual discovery and recruitment acts in single-nest emigrations? Previous empirical work showed the distributions across ants of key behaviors contributing to the collective outcome (Pratt et al. 2005). These include the number of recruitment acts per ant, the number of ants performing each recruitment type, and the number of ants arriving at the new site by different routes. We asked whether our model could replicate the empirical distributions. To answer the question, we simulated the single-nest experiments conducted in (Pratt et al. 2005), on the twelve colonies with compositions detailed in Fig. 10. We used default parameter values, except we increased *search_find* to 0.05. This increase accounts for the presence of only one new nest, hence all "find" actions after the first one are re-discoveries of this nest, which we assume has a higher probability

than finding a previously unknown site (Pratt et al. 2005). In future work, this variable should be expanded to depend on other factors, such as the number of nests in the environment or the spatial geometry. We ran 500 simulations for each colony.

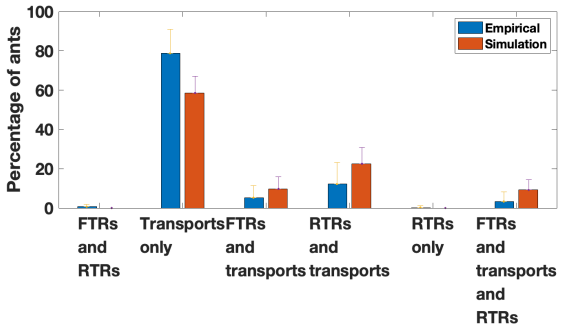
Colony	Nest	Active workers	Passive workers	Total workers	Brood	Total population
1	Thick	46	51	97	141	238
1	Thin	53	53	106	145	251
2	Thick	74	84	158	187	345
2	Thin	66	83	149	190	339
3	Thick	53	33	86	104	190
3	Thin	53	33	86	97	183
4	Thick	63	42	105	60	165
4	Thin	59	40	99	60	159
5	Thick	18	20	38	3	41
5	Thin	37	17	54	8	62
6	Thick	64	30	94	152	246
6	Thin	69	44	113	152	265
$\bar{X}\pm$SD						207±94

Figure 10: Table 2 of (Pratt et al. 2005), showing populations of colonies used in single-nest emigrations to estimate parameters. We ignore the distinction of thick vs. thin nests, and use one set of parameter values to replicate the statistics of individual discovery and recruitment acts.

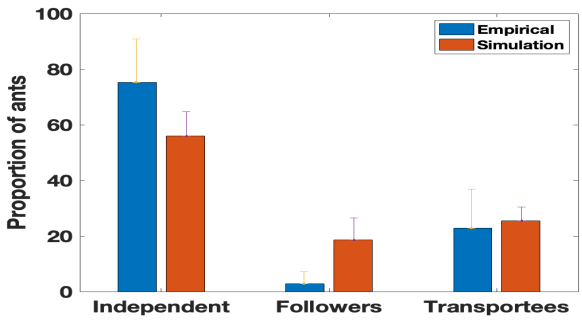
Results We compared the statistics of the model output to the same statistics reported in (Pratt et al. 2005) (Fig. 11). Fig. 11(a) shows the histograms of individual workers grouped by the number of recruitment acts. More than half of the simulated workers never recruited, consistent with the empirical finding of about 60% non-recruiting active workers. The other bins show similar mean and variance to the empirical data. Fig. 11(b) classifies ants by their recruitment behavior, and the breakdowns are again consistent with the experimental observations. Fig. 11(c) categorizes workers by their routes to discovery of the candidate nest, and is again consistent with the findings in (Pratt et al. 2005), at least when the experimental data are pooled over six emigrations by three colonies. However, the distributions across the three different routes vary strongly across emigrations. Indeed, the results in (Pratt et al. 2005) notably differ from those in (Pratt 2005a). While our model does not account for this



(a)



(b)



(c)

Figure 11: Histograms of (a): workers grouped by the number of recruitment acts performed. (b): workers who performed different types of recruitment acts. (c): workers grouped by the route by which workers arrived at the new nest. Blue bars are empirical results from (Pratt et al. 2005). Orange bars show our simulation results. Bar values are averaged over 500 simulations. Error bars show standard deviations.

Colony	Active	Passive	Brood	Total
A4	70	28	228	326
A6	59	74	111	244
A8	62	95	106	263
A14	67	42	192	301
A16	53	88	61	202
A17	73	101	173	347

Table 3: Compositions of colonies used in two-nest emigrations for model validation as shown in Table 3 of (Pratt et al. 2005).

variation, we conclude that it does adequately reproduce key distributions in recruitment behavior in single-nest emigrations.

D.2 Two Unequal Nest: Splits

The second question we ask is: does our model account for the degree of splitting in two-nest emigrations with unequal qualities? In these circumstances, colonies do not always make a unanimous choice, but may temporarily split between the sites before eventually coalescing on a single one. We focus on splitting because it is a primary hindrance to consensus. The measurement of splitting as defined in (Pratt et al. 2005) is the percentage of brood items in the better candidate nest at the time when the last ant has been moved from the home nest.

We replicated the two-nest emigrations in (Pratt et al. 2005), with six colonies whose member compositions are listed in Table 3. We set **nest_qualities** = [0,1,2], representing a destroyed old nest and two candidate nests of mediocre and good quality, respectively. The rest of the configuration parameters were left at the default values.

We ran 500 simulations for each colony, and for each colony we recorded the average percentage of brood items in the better nest at the time the home nest became empty. To compare the simulations with empirical data, we measured for each colony the proportion of simulations departing as far or farther from

Colony	% Pred	%Observed	P
A4	59 ± 17	61	0.86
A6	61 ± 28	80	0.56
A8	63 ± 30	99	0.36
A14	59 ± 20	98	0.1
A16	61 ± 34	100	0.5
A17	60 ± 25	2	0.02

Table 4: Percentage of brood in the better nest for each of the six colonies, predicted vs observed. The last column is the p-value, with $P < 0.05$ indicating a significant difference between predicted and observed percentages.

the colony average as did the experimental value. Twice this proportion gave the p-value for a test of the null hypothesis that the observed value was drawn from the same probability distribution as the simulated values.

Results The results show no significant difference between experiment and simulation for five of six colonies (Table 4). This outcome confirms our model's ability to reproduce observed patterns of splitting in two-nest emigrations for a variety of colony compositions, using the default parameter values.