The Power of Social Information in Ant-Colony House-Hunting: A Computational Modeling Approach

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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. The understanding of these systems and their application can benefit from modeling and analysis of the underlying algorithms. In this study, we define a modeling framework that can be used to formally represent all components of such algorithms. As an example application of the framework, we adapt to it the much-studied house-hunting algorithm used by emigrating colonies of *Temnothorax* ants to reach consensus on a new nest. We provide a Python simulator that encodes accurate individual behavior rules and produces simulated behaviors consistent with empirical observations, on both the individual and group levels. Critically, through multiple simulated experiments, our results highlight the value of individual sensitivity to site population in ensuring consensus. With the help of this social information, our model successfully reproduces experimental results showing the high cognitive capacity of colonies and their rational time investment during decision-making, and also predicts the pros and cons of social information with regard to the colonies' ability to avoid and repair splits. Additionally, we use the model to make new predictions about several unstudied aspects of emigration behavior. Our results indicate a more complex relationship between individual behavior and the speed/accuracy trade-off than previously appreciated. The model proved relatively weak at resolving colony divisions among multiple sites, suggesting either limits to the ants' ability to reach consensus, or an aspect of their behavior not captured in our model.

1. Introduction

Temnothorax ant colonies live in pre-formed cavities such as rock crevices; 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. This work is done by a subset of active ants (about half of the colony's adult workers) who move the remaining passive workers, the queen, and brood items (immature ants) [24, 6, 33].

There are four distinct phases for an active worker in the house-hunting process. First, in the **Exploration** phase, an ant randomly starts to explore her surroundings for a new candidate nest. If she finds one, she enters the **Assessment** phase, where she individually assesses the site's quality according to various metrics [13, 11, 22]. If she is satisfied with the site, she 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 [18, 26, 34]. 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. A canvasser continues leading FTRs until she perceives that the new nest's population has exceeded a threshold, or quorum [23]. 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 [21, 24].

Previous models and experiments indicate that the quorum rule helps the colony to reach consensus rather than splitting among multiple sites [21, 9, 12]. 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. The emigration is completed when all ants in the colony are relocated to the new nest, except possibly for a few active scouts [21].

For this distributed consensus process, 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. An agent-based model has shown that this algorithm helps the colony reach consensus on the best site [24]. Other models have shown how a colony can make a good choice even when no individual directly compares sites [17, 27], and how individual behavioral strategies optimize speed/accuracy tradeoffs at the colony level [7, 15, 16, 20, 25, 32].

Although successful, existing models have been limited to

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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 [3, 29]. 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. To address these issues, we propose a novel role for social information, in which ants directly incorporate nestmate presence into their assessment of nest site quality: more nestsmates at a site increases the perceived quality of that site.

2. Modeling Framework and The House Hunting Model

In this section, we introduce a general modeling "language" that has the potential to be useful for a wide range of applications. We then instantiate this language in the context of the four-phase house hunting process described in Section 1. For details, please refer to [35].

2.1. Model Components

The static entities in the modeling framework are formally defined below. In the house hunting model, an ant is conceptualized to be an agent with a unique *agent-id*, and the environment state is a set of nests (e.g. *env-choices*) each with a distinct physical quality.

- **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*. In the house hunting model, an *external-state* contains: *phase, state_name, role, location*.
- **internal-states**, a set of internal states an agent might be in. Each element in the set is an *internal-state*. In the house hunting model, an *internal-state* contains: *terminate_count, home_nest, candidate_nest, old_candidate_nest*.
- **env-states**, a set of states that the agents' environment might take on. Each element in the set is an *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*.

2.2. Timing Model and Execution

In our modeling framework, the 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.

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 **transitions**, which take the system from configuration $(t-1)$ at time $(t-1)$ to configuration t at time 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 random 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 cannot change 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.

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

2.3. House Hunting Model Parameters and Metrics

House Hunting Model Parameters. After adapting the above framework to the house hunting context, we designed a full set of parameters and their default values as described in [35]. Some important parameters include: **nest_qualities**, which defines the number and qualities of nests in the environment; **lambda_sigmoid**, the increase of which lowers the noise level for individual decisions; **pop_coeff**, the increase of which increases each individual's sensitivity to social information; and **quorum_thre**, which is multiplied by the number of adult ants to give the quorum size. In addition, when a high percentage (**persist_conv**) of the colony converges to a new nest and stays there for **persist_rounds** rounds, we conclude that the simulated emigration has reached *persistent convergence* and stop the run.

Speed Metric. A **convergence score** is the inverse of the round number when a persistent convergence started. If no persistent convergence was reached before the maximum rounds set for the simulation run, the convergence score is 0. Each simulation run has a convergence score.

Accuracy Metric. The average quality of the converged nest across a number of simulation runs. After normalizing the nests' physical qualities such that the best and worst (home) nest has quality 1 and 0 respectively, the **accuracy** of the set of runs is then $\sum_{i \in nests} p_i \times q_i$ where p_i is the proportion of runs that had converged to nest i, which has quality q_i. For the proportion of runs where no convergence is reached (splitting), the corresponding q_i is 0, thus adding 0 to the summation above.

3. Results

Our model is validated against empirical and simulated results in simple 1- or 2- nest environments, as detailed in [35]. In this section, we explore the power of social information on migration speed, accuracy, and cohesion, in two-equal-nest environments. Section 3.1 explores correlations between **pop_coeff** and the degree of randomness in individual decision-making; and Section 3.2 reveals how **pop_coeff** decreases splitting by colonies facing two equal options.

3.1. Balancing Personal and Social Information

Individual ants are capable of directly comparing nests and choosing the better one, but their discriminatory ability is less than that of whole colonies. This may be seen as a kind of "wisdom of crowds," in which the estimations of many noisy individuals are integrated into a more precise group perception. Ants do this via positive feedback loops based on recruitment, which can amplify small differences in site quality [28]. They also use social information via the quorum rule, under which full commitment to a site is conditioned on a minimum number of nestmates "voting" for it by spending time there. The quorum rule inspired us to consider another way that ants might use social information to improve decision-making: by taking population into account when assessing a site's quality. We do this via the parameter **pop_coeff**, which controls the degree to which the presence of nestmates increases a site's perceived value. We propose that this population sensitivity might be able to complement the noisy perception of individual ants, modeled by the parameter **lambda_sigmoid**. We hypothesize that ants may adapt to different values of **lambda_sigmoid** by changing the value of **pop_coeff**. In particular, we sought evidence for a correlation between the values of **lambda_sigmoid** and **pop_coeff** needed to achieve the best convergence score.

To investigate this question, 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 simulated 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. We see evidence of an inverse relation between **pop_coeff** and **lambda_sigmoid** (Fig. 1). For each value of **lambda_sigmoid**, there is a **pop_coeff** value that maximizes the convergence score, and this value increases as **lambda_sigmoid** decreases. Thus, when an individual ant makes noisy local decisions (modeled by low 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**.

There are pros and cons of increasing the value of **pop_coeff**. On the one hand, this introduces a higher momentum in the system and promotes the colony to accumulate population at a certain nest more quickly for faster convergence. In addition, social information via a higher **pop_coeff** might help to break ties among multiple nests by amplifying small random differences in the populations of competing sites, thus preventing splitting. On the other hand, a higher **pop_coeff** can cause 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 a kind of "madness of crowds".

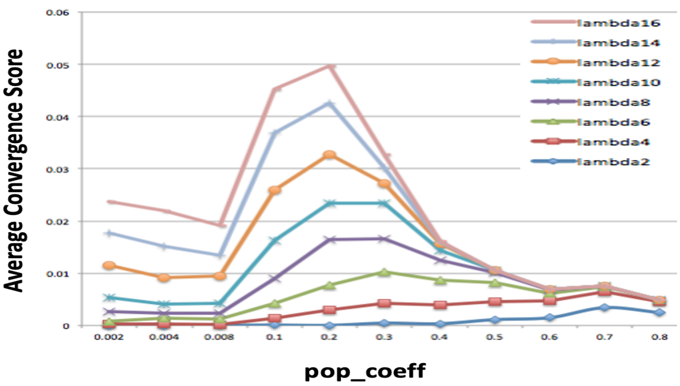

Figure 1: Average convergence score as a function of **pop_coeff**. Different colored curves represent different **lambda_sigmoid** values described in [35].

These trade-offs suggest that there is an optimal value of **pop_coeff** for a given **lambda_sigmoid** as seen in Fig. 1. This predicts that colonies may tune **pop_coeff** according to the uncertainty of individual behavior in order to achieve the highest convergence score for a given environment.

3.2. Avoiding Splits Between Two Equal Nests

In this section we further explore how social information can help colonies to reach consensus when faced with two identical nests. Many social insects have highly nonlinear recruitment mechanisms that lead to symmetry breaking when faced with two identical resources. 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 its pheromone concentration, which leads to rapid amplification of small random differences in the strengths of competing trails [1, 19]. However, similar experiments on *Temnothorax* ants found that they instead exploit both feeders equally, a result that has been attributed to the linear relationship between tandem running effort and recruitment success [31].

An open question is whether this lack of symmetry breaking also holds for nest site selection. If there is symmetry breaking, what are the mechanisms? Does the quorum rule provides sufficient non-linearity to amplify small random differences in site population or are there other unrecognized mechanisms at work? A good candidate for such a mechanism is social information, as discussed in Section 3.1. This would allow amplification of early random differences in population, by increasing the likelihood of recruitment to the nest with more ants. 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, 0.1, 0.2, 0.3, 0.4], in an environment with **nest_qualities** = [0,2,2]. We set **lambda_sigmoid** to 16 in order to be more sensitive to temporal differences in nest populations. From an initial set of simulations, we observed that almost all simulations converged within the default value of **num_rounds**. Therefore, in order to gain more insight into the effect of **pop_coeff** on the degree of splitting before convergence, we reduced **num_rounds** from its default value to 1000. The rest of the parameters take the default values.

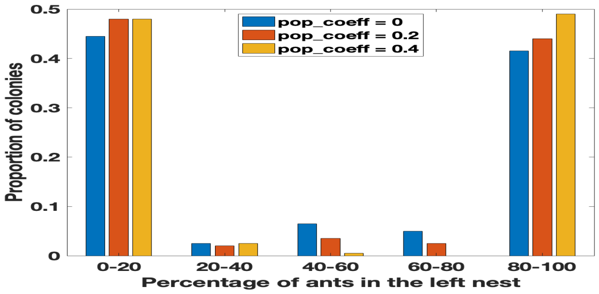

Figure 2: Simulation results for colonies choosing between two identical nests. The histograms show the distribution of the percentage of the colony occupying the left nest, for three different values of **pop_coeff**.

Results. The simulation results show strong symmetry breaking (Fig. 2). 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. 2. This pattern was true regardless of the value of **pop_coeff**, suggesting that the quorum rule is enough to generate 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 preventing them or by facilitating later re-unification.

3.3. Other Predictions: An Overview

Due to space limitations, we present an overview of our other predictions here and leave details in the Appendix.

Confirmation of New Experiments. In Appendix A we consider more complex scenarios where the link between colony patterns and individual behavior has not previously been modeled. For scenarios that have been explored empirically, we determine how well our model can account for observed results. Appendix A.1 examines a colony's ability to choose well when faced with larger option arrays; and Appendix A.2 focuses on how colonies make rational decision time investments depending on nest quality differences.

New Predictions. In Appendix B we use our model to develop new hypotheses and predictions in more complex environments for future experimental study. Section Appendix B.1 gives simulated evidence for a surprising speed-accuracy trade-off for the entire emigration process, tuned by the quorum size; and Section Appendix B.2 discusses colony re-unification after splits with an increasing level of difficulty.

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Appendix A. Confirmation of New Experiments

Appendix A.1. Colonies Have High Cognitive Capacity

How well do colonies perform when selecting from many nests? A previous study [29] 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. 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. A.3). This was true even when the number of nests was increased to 14.

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 [29]: over 80% of individual ants visited only one or two nests in the course of the emigration. Fig. A.4 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. Thus, ants that access many nests have a minor role in the transportation process, supporting the hypothesis that colonies' high cognitive capacity results from avoiding the overloading of individual ants.

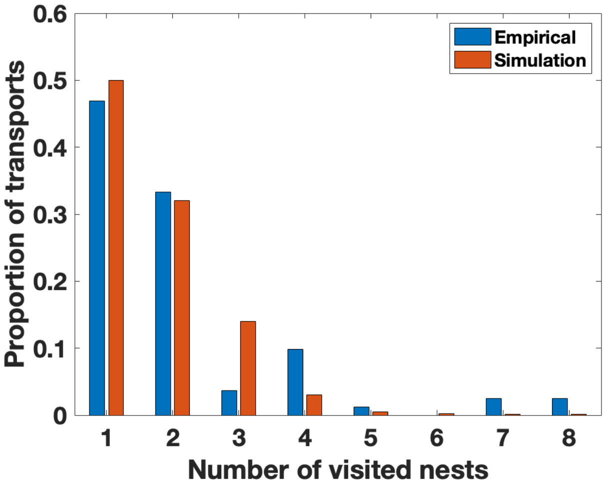


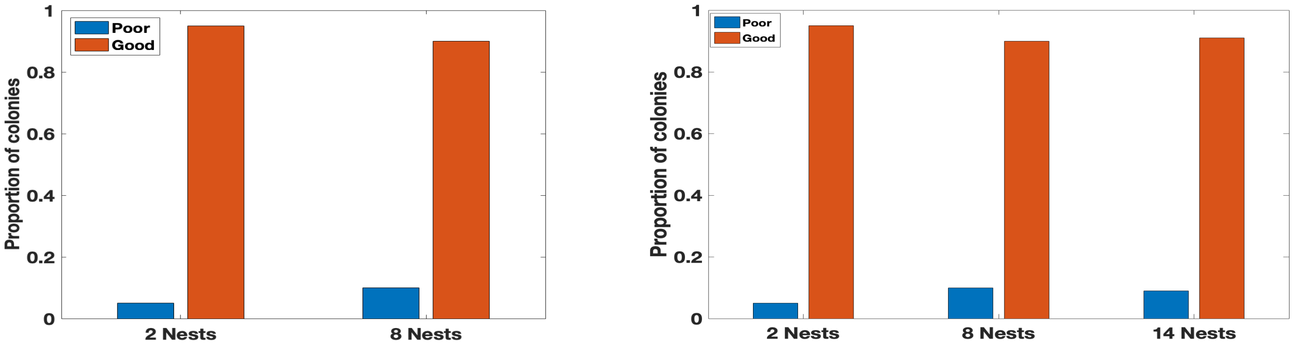
Figure A.4: Proportions of transport efforts as a function of the number of candidate sites visited by each ant. The blue bars show the percentage of transports done by ants that visited a given number of nests [29], and the dark orange bars show the same for simulated ants. Colonies choose among eight nests (four good and four mediocre) in both simulations and experiments [29].

Appendix A.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? Counterintuitively, a previous study [30] 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 [30], 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. A.5). However, at higher mediocre nest qualities, the pattern reverses and



(a) (b)

Figure A.3: The proportions of colonies that eventually moved into poor or good nests. (a): Empirical results in 2-nest and 8-nest settings [29]. (b): Simulation results from our model in 2-nest, 8-nest, and 14 nest settings.

convergence score declines. This basic pattern is seen for all tested values of **lambda_sigmoid**.

We propose that the nest qualities studied in [30] 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 [14]. 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. A.5, 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.

Appendix B. New Predictions

Appendix B.1. Quorum Size and the Speed/Accuracy Trade-off

Temnothorax colonies can adjust their behavior to adaptively trade off the speed and accuracy of decision-making [25, 5]. One of the behavioral tools implicated in this adjustment is the quorum rule. When considering speed, previous studies focused on the time to move out of the old nest, but the completion of an emigration often requires more than that. A fast "first" decision does not always mean a fast emigration. In fact, a low quorum and hence a fast "first" decision could lead to slower emigrations [8] since it could cause more splitting, which the colony must subsequently resolve in a second phase of movement. Here, we explore the effect of quorum size on our speed and accuracy metrics for the whole process. Within the accuracy measure, we pay special attention to the rate of splitting, which is the percentage of emigrations that do not reach a persistent convergence within the given number of rounds. A natural question arises: is there a speed-accuracy trade-off if we define "speed" as (the inverse of) the time taken to the final completion of the emigration? In other words, do the convergence score and accuracy have inverse correlations with **quorum_thre**, and are these relationships affected by splitting rate?

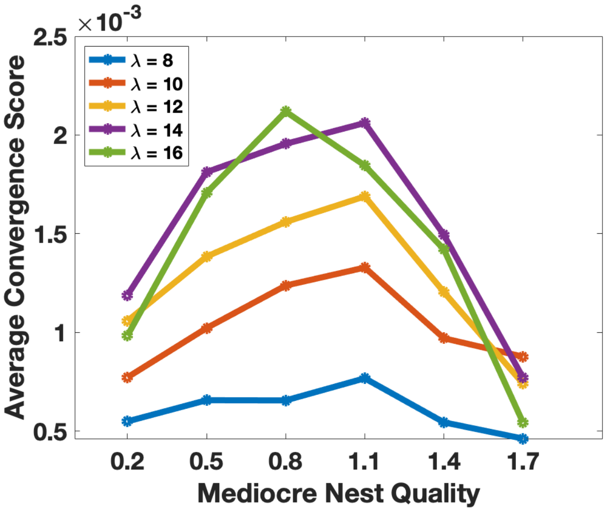


Figure A.5: Average convergence score as a function of the physical_quality of the mediocre nest. The physical_quality of the good nest is 2, and that of the home nest is 0.

We simulated an environment with candidate nests [0.5, 1, 1.5, 2] and a home nest with quality 0 as usual. We used a colony of size 200, consisting of 50 active workers, 50 passive workers, and 100 brood items. Quorum size is assumed to be proportional to the total number of adults in the colony, and is set to **quorum_thre** × **num_adults**. We varied **quorum_thre** from 0.03 to 0.39, and set **pop_coeff** to either 0 or 0.35. We set *num_rounds* to 2000 and ran 100 simulations for each unique combination of **quorum_thre** and **pop_coeff**.

Results. The simulation results show that the convergence score generally has a reverse-U shape that peaks at **quorum_thre** = 0.24-0.27 (Fig. B.6a, Fig. B.6b). In addition, the accuracy measure has a similar shape, but peaks roughly at **quorum_thre** = 0.1-0.15. The split rate, in contrast, has a U-shape, with a trough around **quorum_thre** = 0.15 to 0.18 (Fig. B.6c and B.6d).

The above results indicate a surprising speed-accuracy tradeoff in the segments where the two lines form an "X" shape in Fig. B.6(a) and (b): the increase of **quorum_thre** is accompanied by a decrease in accuracy and an increase in speed. This is the opposite of the findings in related experimental work [25, 5]. However, it is important to note that the current definitions of speed and accuracy differ from those used in the prior work, which defined both quantities only up to the point where the old nest is empty. The results on splitting rate could give more insight into the conflicting results - if repairing splits is costly, lowering the probability of splits by increasing the quorum would indeed significantly increase the average convergence score. But another factor is that setting the quorum too high to reach will also delay convergence. These results point to the need for better understanding of how colonies reunite after splits, as well as the costs of reunification relative to other components of the emigration.

Appendix B.2. Reunification after Splitting

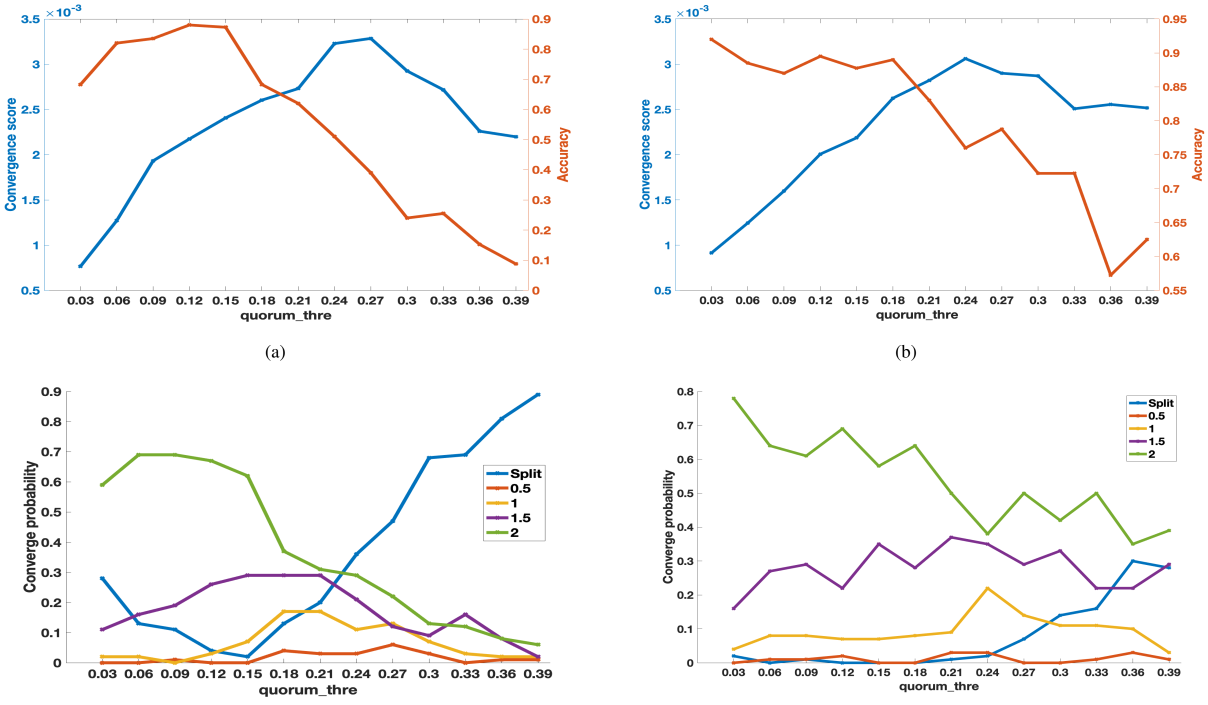
Finally, we touch on another aspect of the robustness of the house hunting algorithm — reunification after splitting. Experimental studies on the speed-accuracy trade-off showed that colonies often split in urgent emigrations, but they also noted that split colonies were eventually able to reunite [10, 8]. Later studies [3, 2, 4] showed that artificially divided colonies readily re-unite, using the same behavioral tools as in emigrations, but relying more on the efforts of a small group of active workers. These findings suggest that emigrations depend on a mixture of individual and colony-level decision making. In this section, we explore how well our model achieves convergence after an arbitrary division among multiple nests. What can we learn about the mechanisms that achieve re-unification?

We ran simulations in which colonies were randomly divided among 2 to 9 nests. At the start of a simulation, each ant's *location* variable in her *ExternalState* was sampled uniformly at random from all *env-choices*. We ran one set of simulations in which one nest was of quality 2 and the rest were of quality 1, and another set in which one nest was of quality 1 and the rest were of quality 2. 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.

Results. As the number of equal quality nests increases, the reunification task becomes increasingly difficult. Additional candidate nests have a negative effect on the convergence score and accuracy of reunification even when they are significantly worse than the best nest in the environment, possibly due to more distractions during evaluations of all nests. But the marginal effect of each additional nest diminishes (Fig. B.7). As a result, the convergence score eventually stabilizes.

However, we see that adding nests of quality 2 (highest quality in the environment) makes reunification much harder since split rate increases quickly. Intuitively speaking, having multiple nests that are the highest quality nest in the environment can greatly intensify competition among them. But this hypothesis needs additional quantitative analyses and empirical confirmation.

In these simulations we randomized the location at the start of our simulations, but not other variables in the internal and external states of individual ants. In reality, when ants are distributed among multiple nests, they most likely have a variety of values for these other variables. We further hypothesize that 1) randomizing the other variables may help with reunification, and/or 2) colonies may have mechanisms to prevent splitting to this extent during the emigration. However, further investigation is needed to test these hypotheses.



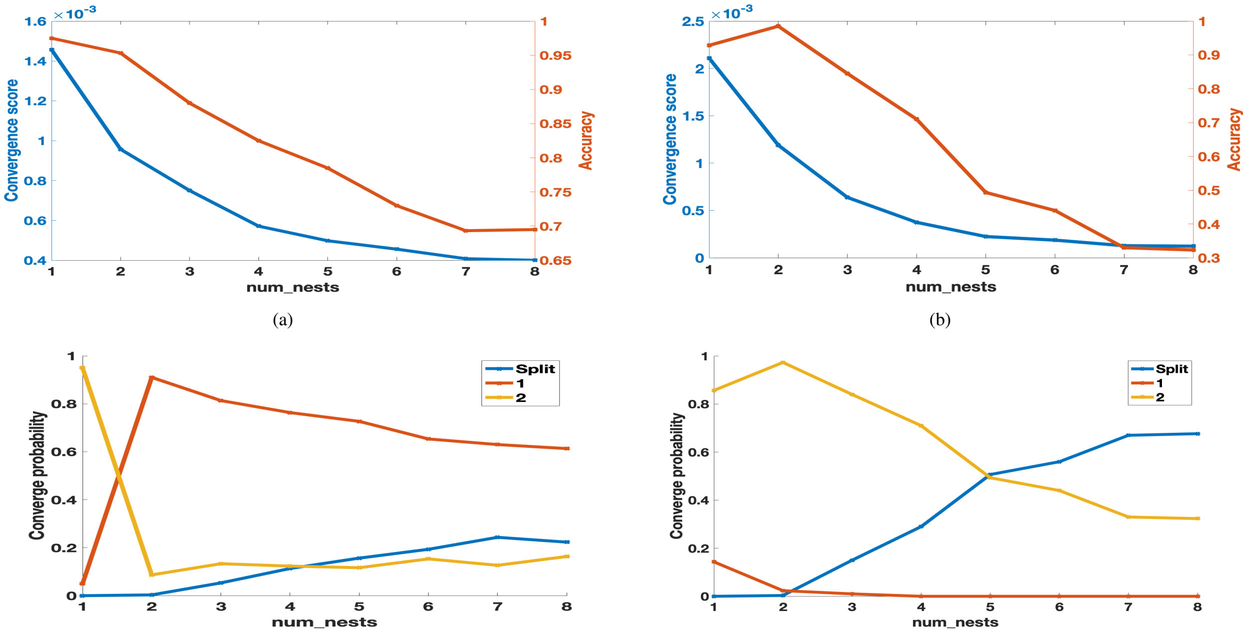
(a)

(b)

(c)

(d)

Figure B.6: (a), (b): Convergence score and Accuracy as a function of **quorum_thre**, with **pop_coeff** = 0 and 0.35 respectively. (c), (d): Probabilities of converging to each nest (or splitting) as a function of **quorum_thre**, with **pop_coeff** = 0 and 0.35 respectively.



(a)

(b)

(c)

(d)

Figure B.7: Convergence scores and splitting for environments with different numbers and qualities of nests. (a) Convergence score and accuracy as a function of the number of nests with quality 1 in the environment. (b) Convergence score and accuracy as a function of the number of nests with quality 2 in the environment. (c), (d) Same environments as (a) and (b), respectively, but plotting convergence probabilities to different nests (or splitting) on the y-axis.