A Comprehensive and Predictive Agent-based Model for Collective House-Hunting in Ant Colonies

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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. Our model successfully reproduces experimental results showing the high cognitive capacity of colonies, their rational time investment during decision-making, and their ability to avoid and repair splits with the help of social information. We also use the model to make predictions about several unstudied aspects of emigration behavior. The results suggest the value of individual sensitivity to site population for ensuring consensus, and they 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. It is our hope that these insights and predictions can inspire further research from both the biology and computer science community.

1 Introduction

Complex biological systems are decentralized systems that have many functionally diverse agents with a global goal, no central control, and many biological constraints. These agents interact with each other locally, selectively, and non-linearly — colony behavior is not simply a sum of individual behavior. Despite their constraints, many biological systems appear to implement algorithms that are robust, noise tolerant, yet efficient in time and communication. Some of the most intricate such algorithms are found in social in-

sects, and they have inspired fascinating engineering designs such as route optimization (the traveling salesman problem) [1], task allocation among robot swarms [2], and mobile sensor networks [3].

In this paper we present a general framework for modeling biological distributed algorithms. We then use this framework to explore a model system in collective decision-making: nest site selection by ants of the genus *Temnothorax*. We aim to show the value of the framework by reproducing the results of earlier models, extending them to account for more recent empirical observations, and making novel predictions to guide future work.

Househunting by *Temnothorax* makes a good subject for modeling distributed algorithms, because these ants have notable collective decision-making abilities whose behavioral underpinnings have been well-studied. Colonies live in pre-formed cavities such as rock crevices or hollow nuts; if their home is damaged, they explore their surroundings for new nests, evaluate each one's quality, determine which is the best, and move the entire colony to their choice [4, 5, 6]. This is a distributed process, in that no single ant knows about all the candidate nests. Instead, their decision emerges from the separate efforts of many scouts, each independently recruiting nestmates to the site it has found. Because recruitment is quality-dependent, better sites accumulate ants more rapidly. 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. Prior models have shown that this algorithm helps the colony reach consensus on the best site [7]. The algorithm can also be quantitatively tuned to emphasize either accuracy (choosing the best nest with high probability) or speed (moving as quickly as possible to minimize danger) [8].

Earlier models of this process are limited in that they explored only 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 multiple sites of varying quality, avoiding splits when candidate nest sites are identical, and resolving colony splits when they occur. 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 that end, a simulator with accurately encoded behavioral rules of individual agents is likely to shed light on various aspects of emergent collective behavior.

Therefore, our first aim is to accurately model the behaviors of individual ants who together produce coherent colony level patterns. By incorporating observed and hypothesized individual level behaviors into the model, computer simulations can predict the collective properties of the group. Close comparison with biological experiments on individual and colony behavioral statistics then provides validation on the hypothesized individual behaviors and local rules.

Secondly, we use our model to investigate questions that have incomplete experimental results or none at all. These questions include: 1) How does colony performance change as the number of nest options increases? 2) How do nest quality differences affect the speed of decision making? 3) How does social/peer information affect the speed of finishing the entire emigration when facing equal options? 4) How does social/peer information affect the probability of splitting when facing equal options? 5) How does the quorum threshold affect the speed-accuracy trade-off, where both metrics are defined for the whole process instead of only for when the old nest becomes empty? 6) How well do colonies re-unify at one location if individuals are dispersed among many nests?

Our model touches on several aspects of the emergence of collective intelligence in the house hunting process, but many more are yet to be explored. Therefore one final important goal of our simulator is to provide a versatile, easy-to-use and maintainable modeling tool that can be used to quantitatively test more hypotheses that we may not have included in this paper. From an engineering perspective, such tools can lead to better understanding of the roles of local rules to achieve a global phenomenon. From a biology perspective, they can inspire and provide directions to new experiments in future research. From a theoretical perspective, our simplified model (compared to earlier models) opens the door to rigorous proofs on convergence speed/accuracy.

The rest of the paper is organized as follows: Section 2 defines a general framework that we believe will be useful not only for this algorithm but for other agent-based distributed algorithms as well. Section 3 applies this framework, with designs and interpretations specific to the house hunting context. Section 4 describes our Python implementation of the house hunting simulator, instructions on running simulations, and their scoring goals and metrics. Section 5 validates our model with experimental statistics on individual behaviors and the collective properties of the colony. These validations give us confidence in the accuracy of our model as we proceed into further predictions of colony behaviors listed in Section 6. These predictions show promising simulated results but have limited or nonexistent experimental verification. It is our hope that biological experiments can be done later, to test the hypotheses shown by our simulations. Finally, Section 7 summarizes our results and proposes possible future research directions.

2 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 Section 3 we instantiate this language in the context of the house hunting process in ant colonies.

2.1 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 par-

ticular 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.

2.2 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 [9, 10], 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.

2.3 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* information 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 [11, 12, 13, 7].

3 House Hunting Model

This section uses the framework defined in Section 2 to describe the house-hunting process.

3.1 Informal Description

An ant 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 simply transported to the new nest by active workers [7, 14].

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 [15, 16, 17]. 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 [18]. 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 [19]. 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 [14, 7]. Previous models and experiments indicate that the quorum rule helps the colony to reach consensus rather than splitting among multiple sites [5, 20, 21]. 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 [22, 20]. 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 [19]. 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 10 as an upper-bound estimate.

The emigration is completed when all ants in the colony are relocated to the new nest, except possibly for a few active scouts [5].

3.2 Formal Model

3.2.1 Model components

In this section, we show how each component in our modeling framework (Section 2.1) is defined in the house hunting algorithm context.

Fig. 1 shows our native data structures as used by various components in the system: *Nest* objects,

```
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 1: Native data structures that define different entities in the distributed system.

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. 1. 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 Section 2.1. Note that for consistency with our implementation in Section 4, we use -1 or an empty string "" to represent any invalid default integer or string values represented by $\perp$ in Section 2.

- **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 *ExternalState* 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 carrying 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 Section 3.2.3. 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
```

  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 Section 4.1.
- **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) ∪ -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 Section 2.1. 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 Section 2.1. Refer to Section 3.2.2 for details.
- **transition**(*agent-id, state, all-external, action*): the same function as defined in Section 2.1. Refer to Section 3.2.3 for details.

3.2.2 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 Section 4.1.

- 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 $terminate_count \geq 10$, $\tilde{a}$ 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 $terminate_count \geq 10$, $\tilde{a}$ 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 $p(x)$. All other *action-type*'s have 0 probability. Both variables x' and

ec take the invalid default value -1 with probability 1. To determine $p(x)$, an ant is required to assess the quality of a nest in the environment. The assessment of the quality of a nest includes both its physical qualities [23, 24] and the nest population [25, 22]. Therefore, we use a simple linear combination of these two values to denote the final nest quality with a new parameter called **pop_coeff** as the coefficient of the population effect. In other words, the final nest quality of a nest with *physical_quality* q and population *pop* (obtained from *all-external*) is

$$\frac{q}{4} + \textbf{pop_coeff} \times \frac{pop}{num_ants}, \tag{1}$$

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, and bring $p(x)$ closer to a step function.

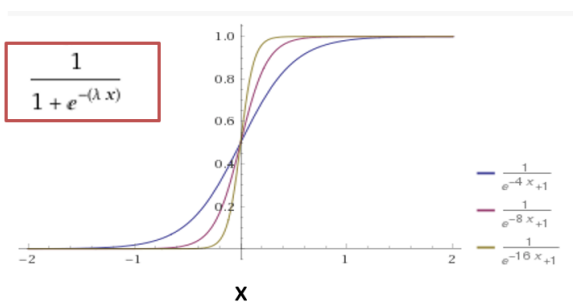


Figure 2: Sigmoidal function with $\lambda = 4, 8, 16$

- 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 (Equation 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. To determine $p(x)$, an ant x is required to compare the quality of its *candidate_nest* (with physical_quality q_1 and population pop_1) and its *home_nest* (with physical_quality q_0 and population pop_0). We still use the sigmoidal function in Equation 2, with 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.

3.2.3 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 [5, 14].

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

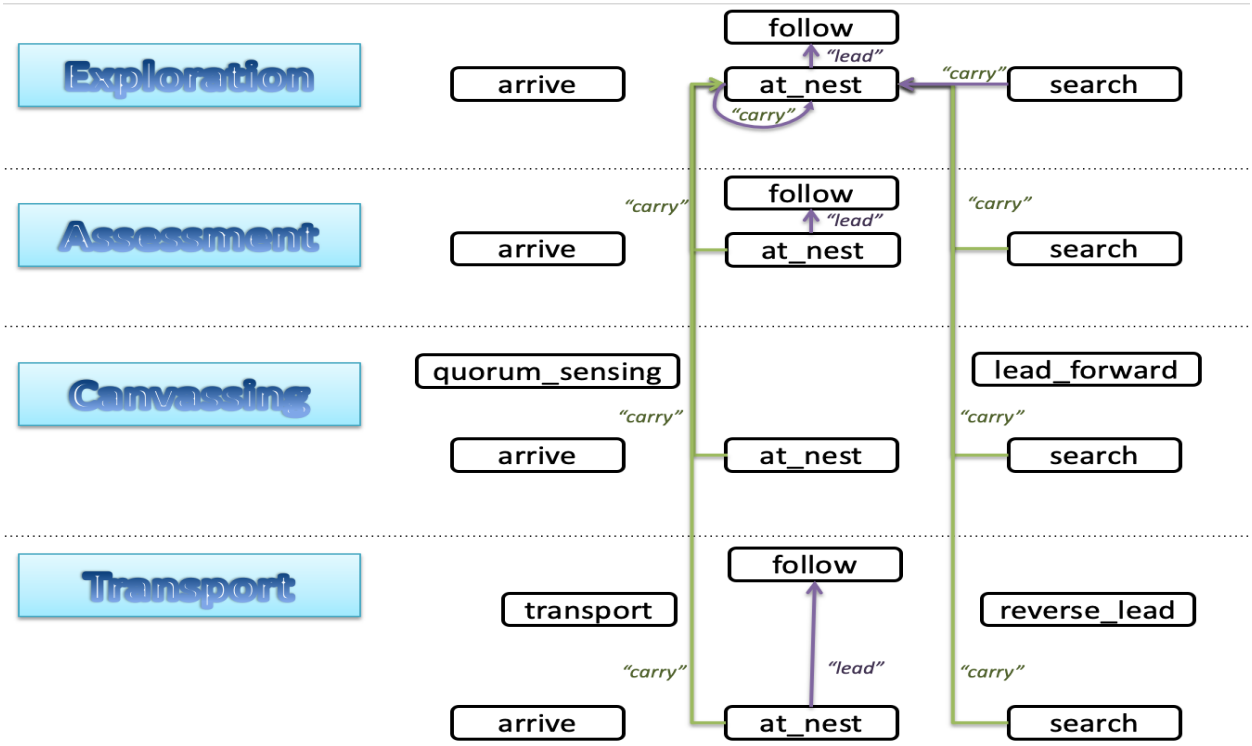
old_candidate_nest are set to -1 as the default invalid value. And *terminate_count* starts with 0.

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 Section 3.2.2 - 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 3.1. 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 2.2).

- 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. 3a, 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*.



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

Figure 3: States and actions modeling the behavior of active ants responsible for organizing colony emigrations. As described in Section 3.1, the four distinct phases are in different boxes: Exploration, Assessment, Canvassing, and Transport.

- 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. 3b, 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*.

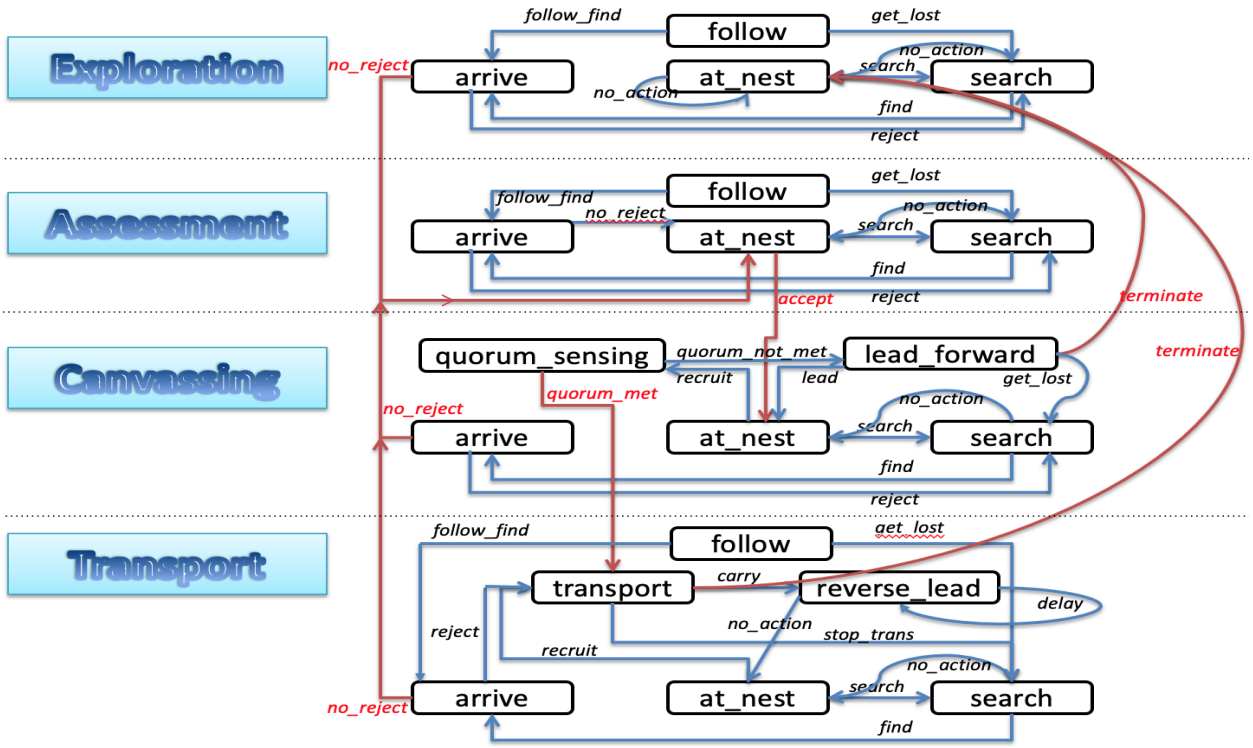
We now walk through all *state_name*'s and their *action-type*'s in Fig. 3a and Fig. 3b in a phase by phase fashion. In the figures, *action-type*'s are color-coded as shown in Table 1.

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

Table 1: Color coding of arrows representing *action-type*'s in Fig. 3a and Fig. 3b.

Exploration

- An ant in at_nest_E has four possible actions. First, she can perform "no_action" and remain



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

Figure 3: (Cont.) States and actions modeling the behavior of active ants responsible for organizing colony emigrations. As described in Section 3.1, the four distinct phases are in different boxes - Exploration, Assessment, Canvassing, and Transport.

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 sub-scripted 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 $transport_T$.

4 Model Implementation and Simulation

We implement the model described in Section 3 in Python, with one configuration file that contains all the parameters in the model.

4.1 Configuration File

Below is an example configuration file. There are three kinds of parameters: environment, algorithm, and settings. The values below for each parameter are the baseline default values we use for our simulations.

```
[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
```

Environment parameters are controlled by the environment and not considered changable or tune-able. 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 that we can manipulate in order to change the *select-action* function and hence the outcomes of our simulations. These include the lambda 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 continued transports instead of stopping transportation. Related explanations are in Section 3.2 and 3.2.2.

Settings parameters control plotting features and also convergence criteria. The setting in the default configuration file shown here means that we would like the program to generate a plot of one simulation run. The maximum number of rounds is 4000 in this run. And we conclude **convergence** if 90% of the

colony population (not necessarily the same 90%) are in a new nest. If this lasts for at least 200 rounds in the same nest, we terminate the simulation and conclude that the simulation has reached a **persisted convergence**.

Baseline Default Parameter Values Compared to the agent-based model in [7], our model places less emphasis on assigning specific observed values to a large number of parameters, but rather on a simple and elegant model that is more agile to a wider range of possible behaviors. For that reason, some of the parameter cannot be directly drawn from existing empirical data. We estimate these parameter values in a trial-and-error fashion until simulation results matches well with the empirical results in [7]. These baseline values are used as a default throughout Section 5 and 6, unless otherwise specified.

The sources for determining the parameter values are listed in Table 2. 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** × (num_active+num_passive) + **quorum_offset**) is observed to have a median value between 4 and 18 ants on worker sizes from 24 to 150, with the quorum size having a significant positive correlation with the number of adult ants [5, 21]. Therefore, with a colony of size 200 (adult worker size 100), we choose to use **quorum_thre** to be 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. These nuances are not captured in our model in the interest of simplicity. But they can significantly affect the simulation outcomes, and are an important future extension of our work. 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 neither ant gets lost. It is observed that individual tandem runs have a high successful rate ranging from 61% to 94% allowing 1 minute re-connect time after a contact loss [26]. And given enough time a higher percentage of followers find the destination nest [27], however possibly through a new search. We thus use 0.9 as our FTR success rate. 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*, is designed to model the slower speed of an FTR, 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 search around her area. 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, and we picked 0.7 to be our baseline value.

Parameter	Value	Source
lambda_sigmoid	8	trial-and-error, Sec. 6.3
pop_coeff	0.35	trial-and-error, Sec. 6.3
quorum_thre	0.15	[5, 21]
quorum_offset	0	[5]
search_find	0.005	trial-and-error
follow_find	0.9	[26, 27]
lead_forward	0.6	trial-and-error
transport	0.7	[7]

Table 2: Default parameter values and the sources that helped determine these values.

In addition, we believe that an average colony size of 200 with 50 active, 50 passive, and 100 brood items is within reasonable range of real colony compositions [21]. 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. The values for variables **percent_conv** and **persist_rounds** are determined by discussion and our rough estimates from past empirical observations.

4.2 Speed and Accuracy Measures

We define the speed and accuracy 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. More specifically, if convergence has been reached in one simulation run, we design the **convergence score**, to be the inverse of the round number when a persisted convergence started. If no persisted convergence was reached before the end of the simulation, the convergence score is 0. Each simulation run has a convergence score.

Accuracy Another important metric is **accuracy**, which is defined for a group of simulation runs. This metric tells us how well the colony is at selecting the best choice in the environment to emigrate to. Thus, each of the nest options in the configuration has an empirical probability of the colony converging to it, called the nest's **convergence probability**. Note that we also get a probability of splitting. To calculate the final accuracy, we also normalize the nests' physical qualities, such that the best nest has quality 1 after normalization, and the worst nest which is the home nest still has quality 0. The **accuracy** of the configuration is then

$$\sum_{i \in nests} p_i \times q_i$$

where p_i is nest i's convergence probability, and q_i is its normalized physical quality. If no convergence is reached (splitting), the corresponding physical quality to that probability will be 0, thus not contributing to the summation above. Our accuracy metric is not defined for any individual simulation run.

4.3 Data Structures and Global Variables

We define four native data structures, as shown in Fig. 1. The global variables include 1) the transition tables defined in Fig. 3, 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.

4.4 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 *round*s, 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_id*s 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 3.2.3, 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.

5 Model Validation

We begin by validating our model against the same empirical data that was successfully accounted for by two earlier models [7, 8]. First, we 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. Finally, we investigate how colonies trade off speed and accuracy depending on the urgency of their move. For all scenarios, we simulate the same data explored by the earlier models, and compare our results, at both individual and colony level, to the empirical observations.

5.1 Single-Nest Emigrations

The first question we ask is: does our model accurately account for statistics on individual recruitment acts in single-nest emigrations? Previous empirical work showed the distributions across ants of key behaviors contributing to the collective outcome [7]. These include the numbers of recruitment acts per ant, the numbers of ants performing each recruitment type, and the numbers 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 [7], on the six colonies with compositions detailed in Table 3. We used default parameter values, except we increased *search_find* to 0.05. This increase is because for any individual ant, all "find" actions after the first time are discovering the nest that she already knows, which has a much higher probability [7]. This causes an overall higher "average" value for *search_find*. 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.

Results We compared the resulting statistics to the same statistics reported in [7] (Fig. 4). Fig. 4(a) shows the histograms of individual workers grouped by the number of recruitment acts. We see that more than half of the workers never recruited, consistent with the findings in [7] that show a little over 60% non-recruiting active workers. The other bins also show similar mean and variation trends. Fig. 4(b) details the types of different worker ants, classified by their recruitment behavior, and the breakdowns are again consistent with the statistics gathered from biological experiments by [7]. Fig. 4(c) shows the percentages of workers categorized by the routes of discovery of the candidate nest. The results show consistency with the findings in [7] which contain biological experiments pooled over six emigrations by three colonies. However, the proportions of the three different routes vary a lot across emigrations - the results of the biological experiments from [7] differ significantly from those from [28]. So we do not make any stronger claims on the proportions of these three different discovery routes here.

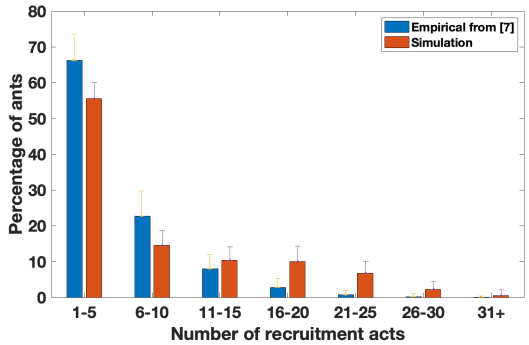
From the above results, we have validated that the mechanisms that cause the different distributions in recruitment behavior in single-nest emigrations are correctly captured in our model.

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

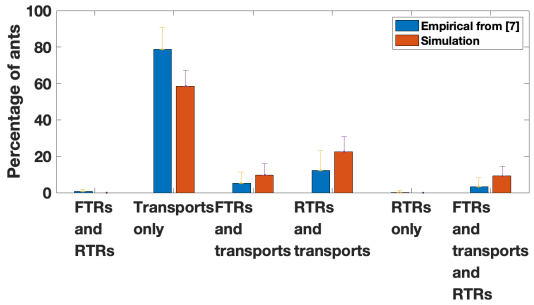
Table 3: Compositions of colonies used in two-nest emigrations for model validation as shown in [7].

5.2 Two Unequal Nest: Splits

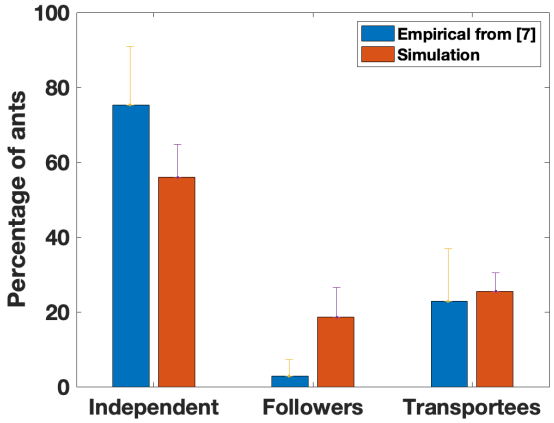
The second question we ask is: does our model account for the degree of splitting in two-nest emigrations with unequal qualities? In these circumstances, colonies do not always move unanimously into a single nest, but may temporarily split between them before eventually coalescing on a single nest. We focus on splitting because it is a primary hindrance to consensus. We measure splitting as the percentage of brood items in the better candidate nest at the time when the home nest first becomes empty.



(a) Histogram of workers grouped by the number of recruitment acts performed.



(b) Histogram of workers who performed different types of recruitment acts.



(c) Histogram of workers grouped by the route by which workers arrived at the new nest.

Figure 4: Blue bars show our simulations. Orange bars are results from [7]. Bar values are averaged over 500 simulations. Error bars show standard deviations.

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.

We replicated the two-nest emigration tests from [7], 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 are left at default value.

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 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 validates our model's ability to reproduce observed patterns of splitting in two-nest emigrations for a variety of colony compositions.

5.3 Two Unequal Nests: Speed-Accuracy Trade-off

The third question we ask is: does our model reflect the way that colonies trade off speed and accuracy when the urgency of the emigration changes? In "urgent" situations, ants face a critical need for immediate new shelter and thus would prefer to move out of the old nest location as fast as possible. In contrast, in less urgent situations they can deliberate longer among alternatives to increase the likelihood of moving directly to the best site [8, 29]. Experiments have adjusted urgency by offering colonies a choice between a mediocre and a good nest under two circumstances: their old nest has just been destroyed (high urgency) or their old nest is of acceptable quality but worse than either of the new candidates (low urgency). Our simulations followed the same tactic by tuning the physical quality of the home nest to adjust urgency. Does our model exhibit the above behavior?

To verify this, we ran 300 simulations each for eleven home nest qualities in range [0,1], with candidate nest qualities of [1,2]. We used the default parameter values, except **lambda_sigmoid** which is set to 16 in order to increase the ants' sensitivity to home nest quality differences, and we set **pop_coeff** to 0 in order to compare results with those from [8]. As in [8], we measured the duration of emigration as the time in rounds at which the old site was completely abandoned and the accuracy of decision-making as the proportion of the colony's members inside the good site at the time of old nest abandonment.

Results The results show that time that it took to complete an emigration increased as urgency decreased (i.e., as old nest quality increased) (Fig. 5b). This is consistent with the empirical observation that higher urgency induces faster emigrations (Fig. 5a). Furthermore, the simulations show that higher urgency (lower old nest quality) reduces the likelihood of the colony achieving consensus on the better site. This also matches the empirical results, which show that higher urgency leads to lower accuracy [8].

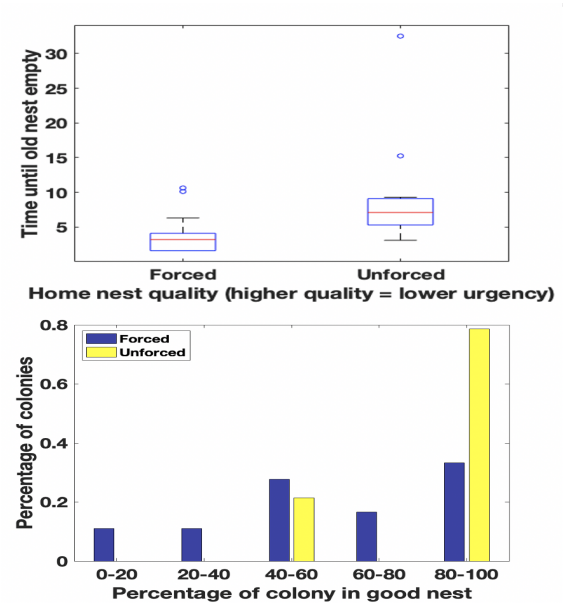
These results confirm that our model can account for the empirically observed speed and accuracy trade-off up to old nest abandonment. However, it is worth noting that real colonies in the low urgency situation were better able to reach consensus than our simulated colonies. This might suggest that our model relies more on reunification after splits in order to achieve consensus, or that there are other mechanisms at work that this experiment failed to capture, such as a non-zero *pop_coeff*.

6 Model Predictions

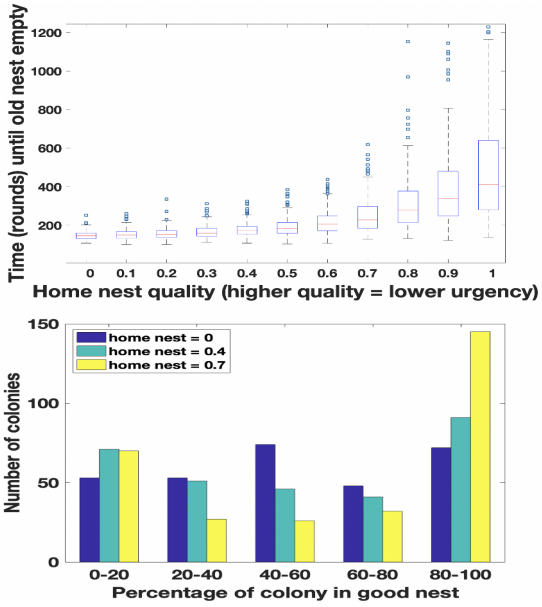
In this section we consider more complex scenarios where the link between colony patterns and individual behavior has not previously been modeled. For scenarios that have been explored empirically, we determine how well our model can account for observed results. We also use our model to develop new hypotheses and predictions for future experimental study. All simulations in this section default to the configuration file described in Section 4.1, unless specified otherwise.

Please note that since our model places a heavy focus on the feedback between individuals and colonies as a tie-breaking mechanism, we did not use the model to predict behaviors of any one individual ant without being part of a larger colony and being influenced by any of her colony members. The research to understand how individual ants achieve phase transitions and make decisions without being able to assess colony features (such as the number of nest mates) is beyond the scope of this paper.

The rest of the section is organized as follows: Section 6.1 shows consistent experimental and simulated evidence of how colonies can achieve higher probability emigrating to the best nest (a.k.a. higher accuracy) in complex environments; Section 6.2 focuses on how nest quality differences can affect the speed of emigrations in a two-nest environment. Section 6.3 discusses the correlations between **pop_coeff** and different levels of randomness in individual decision-making. Section 6.4 reveals how **pop_coeff** decreases the degree of splits when facing two equal options. Section 6.5 gives simulated evidence for a surprising speed-accuracy trade-off for the entire emigration process, tuned by the quorum size. Finally, Section



(a) From [8]: Speed and accuracy of decision-making in forced and unforced emigrations. (Top) Time until the old nest is empty for each treatment. The ends of each box mark the upper and lower percentiles, and the horizontal line inside the box gives the median. The brackets show the data range, and circles are outliers. (Bottom) Histograms of the degree to which colonies split between the good and mediocre new nest sites, for forced (blue bars) and unforced (yellow bars) emigrations.



(b) Both top and bottom plots are the same as (a), but the results are from simulations of our model, and the results are more quantitative. (Top) Higher home nest quality is equivalent to less urgency in starting the emigration (more "unforced"). (Bottom) The same histogram as in the bottom plot of (a), but with more home nest quality options.

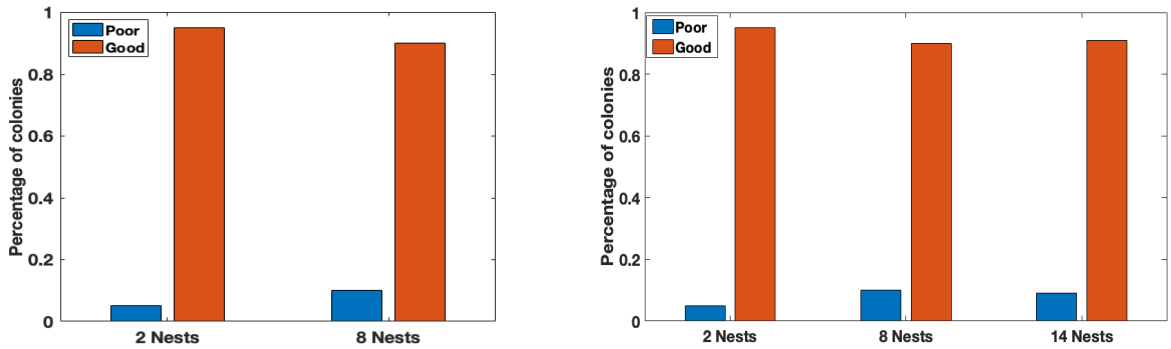
Figure 5

6.6 discusses colony re-unification after splits with an increasing level of difficulty.

6.1 Colonies Have High Cognitive Capacity

How well do colonies perform when selecting from many nests? A previous study [30] 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 poor (physical_quality 1.0) and the rest of which are good (physical_quality 2.0). We considered three environ-



(a) Empirical results in 2-nest and 8-nest settings [30].

(b) Simulation results from our model in 2-nest, 8-nest, and 14 nest settings.

Figure 6: The percentages of colonies that eventually moved into poor or good nests.

ments 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. 6). 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. Simulation results in the 8-nest environment resonate with empirical results shown in Fig. 7 [30]. Over 80% of individual ants visited only one or two nests in the course of the emigration. A 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.

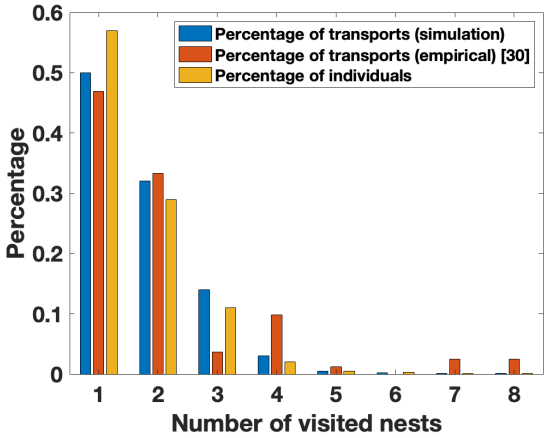


Figure 7: Percentage of transports and percentage of ants as a function of nest visits. Blue and dark orange bars are the percentage of transports done by ants who visited different number of nests during the emigration, both in the 8-nest environment with 4 good and 4 mediocre nests. Blue bars are for our simulated results, and dark orange bars are empirical results from [30]. Light orange bars show the distribution of individuals according to the number of nests they visited.

6.2 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 [31] 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 λ values: [8,10,12,14,16].

Results If our model reproduces the rational time investment choices of colonies [31], 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. 8). However, at higher mediocre nest qualities, the pattern reverses and convergence score declines. This basic pattern is seen for all tested values of λ.

We propose that the nest qualities studied in [31] 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 [32]. 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. 8, 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.

6.3 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 [33]. 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 site population into account when

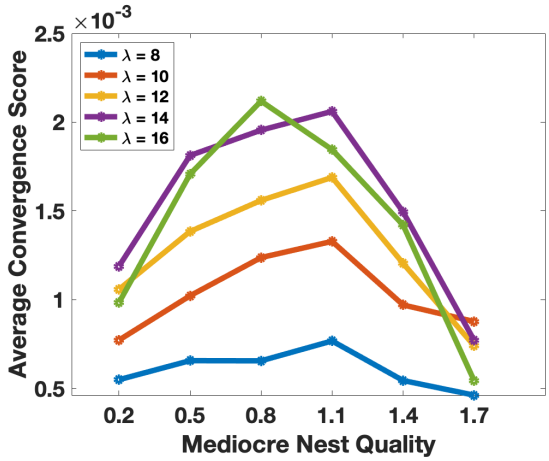


Figure 8: Average convergence score as a function of the physical_quality of the mediocre nest. The physical_quality of the good nest is 2, and that of the home nest is 0.

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 λ in the Eq. 2. We hypothesize that the colony can adjust to different values of λ by changing the value of **pop_coeff**. In particular, the research question of interest is: to achieve the highest convergence score, does **pop_coeff** have significant correlations with the value of λ, and if so, what kinds of correlations?

To investigate this question, we ran simulations for different combinations of **pop_coeff** (ranging from 0.002 to 0.8) and λ (ranging from 2 to 16). We ran simulations for two environments containing two identical new nests [0,1,1]. For each combination of **pop_coeff** and λ, 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 λ (Fig. 9). For each value of λ in the range [2,16], there is a value of **pop_coeff** that maximizes the convergence score, and this value increases as λ decreases. Thus, when an individual ant makes noisy local decisions, she can counteract this deficiency by relying more on the input of her peers through a higher value of **pop_coeff**.

However, a high value also has risks. Below we discuss our interpretation of 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. Social information 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 a optimal value of **pop_coeff** for a given λ as seen in Fig. 9. 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.

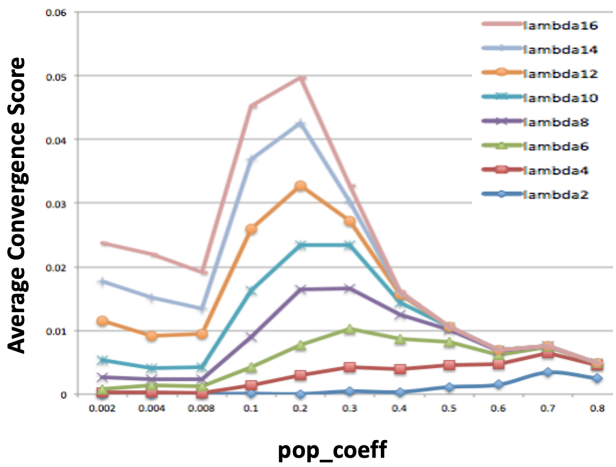


Figure 9: Average convergence score (across 500 simulations) as a function of **pop_coeff**. Different colored curves represent different λ values as described in the individual decision model (Fig. 2). This shows that the optimal value of **pop_coeff** increases as λ decreases.

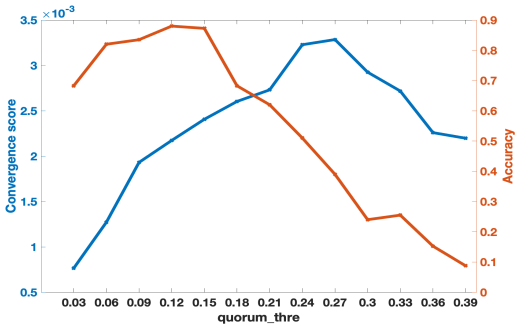
6.4 Avoiding Splits Between Two Equal Nests

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 the amount of pheromone it contains, which leads to rapid amplification of small random differences in the strengths of competing trails. 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.

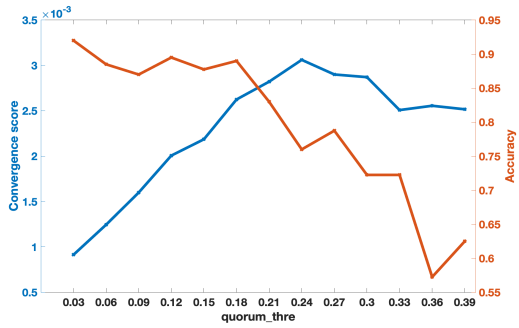
An open question is whether this lack of symmetry breaking also holds for nest site selection. When presented with identical nests, do colonies choose only one or split between them? One possibility is that the quorum rule provides sufficient non-linearity to amplify small random differences in site population, thus ensuring that the colony does not split. Another possibility is that colonies have some other as of now unrecognized mechanism of avoiding splits. A good candidate for such a mechanism is incorporation of site population into each scout's assessment of site quality, as discussed in Section 6.3. 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 converge within the default value of **num_rounds**. Therefore in order to gain more insights on the effect of **pop_coeff**, we set it to a smaller value 1000. The rest of the parameters take the default values.

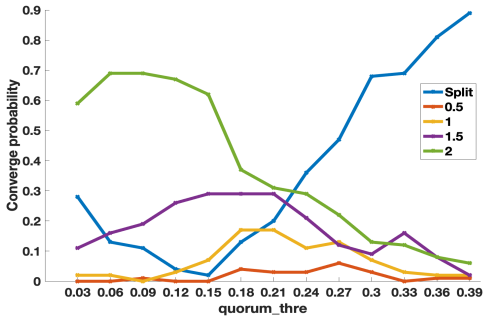
Results The simulation results show strong symmetry breaking (Fig. 11). That is, a large majority of simulations ended with 80% to 100% of the colony in one of the two nests. When consensus was reached, it was roughly equally likely to be in nest 1 or nest 2, producing the distinctive U-shaped distribution seen in Fig. 11. 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 prevention or by facilitating later reunification. These mechanisms can have significant effects in more challenging environments with more candidate nests.



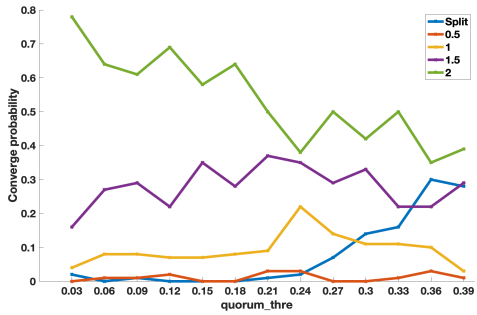
(a) **pop_coeff** = 0. Speed and accuracy.



(b) **pop_coeff** = 0.35. Speed and accuracy.



(c) **pop_coeff** = 0. Probabilities of converging to each nest.



(d) **pop_coeff** = 0.35. Probabilities of converging to each nest.

Figure 10

6.5 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 [8, 29] (Section 5.3). One of the behavioral tools implicated in this adjustment is the quorum rule. Colonies lower the quorum in more urgent situations, increasing their reliance on individual judgement. This allows them to make rapid decisions and quickly move the colony out of the old nest, at the cost of an increased probability of splitting or choosing an inferior nest [34, 35].

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 [35] 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 the speed and accuracy as we have defined for the whole process (Section 4.2). Within the accuracy measure, we pay special attention to the split rate, 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 split rates?

We simulated an environment with candidate nests

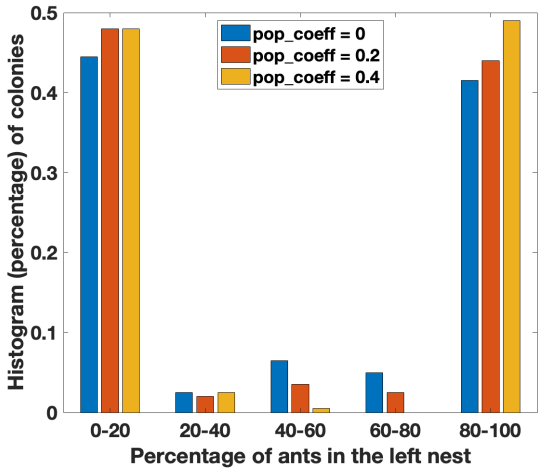


Figure 11: Histogram (percentage) of the number of ants in the left nest, with results from experiments and simulations.

[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**.

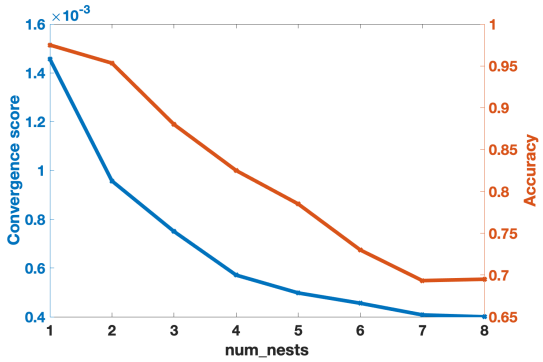
Results The simulation results show that the convergence score generally has a reverse-U shape that peaks at **quorum_thre** = 0.24-0.27 (Fig. 10a, Fig. 10b). In addition, the accuracy measure has a similar shape, but peaks roughly at **quorum_thre** = 0.1-0.15. The split rate, in contrast, has a U-shape, with a trough around **quorum_thre** = 0.15 to 0.18 (Fig. 10c and 10d).

The above results indicate a surprising speed-accuracy trade-off in the segments where the two lines form an "X" shape in Fig. 10(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 our findings in Section 5.3 and in the related experimental work [8, 29]. 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 split rate could give more insight into the conflicting results - if split repairs are costly, lowering the probability of splits by increasing quorum would indeed significantly increase the average convergence score. But another factor is that if the quorum is too high to reach, it also delays convergence. We conclude that it is essential to investigate more about the little-known split repair process and its relative cost to other sub-processes in the entire emigration.

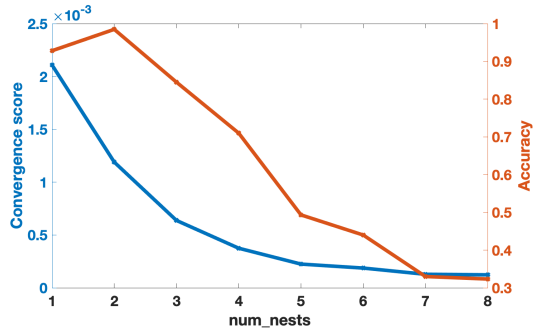
6.6 Reunification after Splitting

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 [34, 35]. Later studies [36, 37, 38] 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 the robustness and flexibility of the algorithm. They show 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?

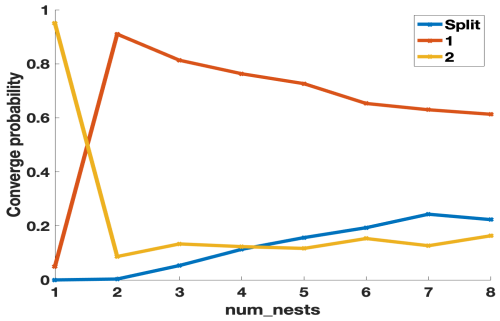
We ran simulations in which colonies were randomly divided among 2 to 9 nests. At the start of a simulation, each ant's *location* variable in her *ExternalState* was sampled uniformly at random from all *env-choices*. We ran one set of simulations in which one nest was of quality 2 and the rest were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



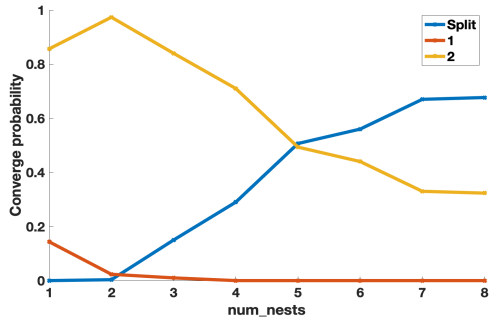
(a) Convergence score and accuracy as a function of the number of nests with quality 1 in the environment, with random start.



(b) Convergence score and accuracy as a function of the number of nests with quality 2 in the environment, with random start.



(c) Convergence probabilities to different nests as a function of the number of nests with quality 1 in the environment, with random start.



(d) Convergence probabilities to different nests as a function of the number of nests with quality 2 in the environment, with random start.

Figure 12

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, but the marginal effect of each additional nest diminishes (Fig. 12). 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.

Please note that here we only 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) the ant colonies may have mechanisms to prevent splitting to this extent during the emigration. However, further investigation is needed to test these hypotheses.

7 Future Work

Our model captures many aspects of individual behavior, but it leaves out some important timing features. These include 1) effects of the spatial distribution of nests, 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 can shed more light on the timing of individual actions. In addition, these may reveal important hidden variables and their influence on current variables such as *search_find*.

On the analysis side, there are many exciting directions for further research. First, we note the link between the effects of different quorum sizes and the models mentioned in [32]. Specifically, it is possible that tuning quorum sizes can change the weights of the two different decision models in [32]. This prompts an interesting analytical project for our readers, to derive a more quantitative model that combines the tug-of-war model and the horse-race model based on the same factors that affect how a colony chooses the most beneficial quorum size.

Secondly, our model suggests that individual ants take account of site population when assessing a site, but this has not been experimentally established in actual ants. Empirical testing of this idea would be highly valuable. Our results suggest that it may be important for preventing and repairing split decisions. However, the amount of social information that individuals should rely on is an intricate balance, as we described in Section 6.3. Quantitatively acquiring the range of possible splits provided the value for **pop_coeff** would be extremely valuable in further analysis on the speed and accuracy bound of the algorithm. A related research direction is to find out other factors that allow colonies to robustly reunify in split cases.

Thirdly, the predictions we made in Section 6 are intriguing with carefully designed control environments, but mostly from simulation results. To draw more solid conclusions, we strongly urge our readers from the biology community to conduct corresponding empirical experiments and provide more detailed biological insights.

Finally, our modeling framework can be flexibly adapted to other distributed algorithms inspired by animal groups. It also serves as a stepping stone for more rigorous mathematical formulations and proofs of guaranteed bounds on any metrics of interest.

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