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

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Abstract

The decentralized cognition of animal groups is both a challenging biological problem and a potential basis for bio-inspired design. The understanding of these systems and their application can benefit from modeling and analysis of the underlying algorithms. In this study, we define a modeling framework that can be used to formally represent all components of such algorithms. As an example application of the framework, we adapt to it the much-studied house-hunting algorithm used by emigrating colonies of *Temnothorax* ants to reach consensus on a new nest. We provide a Python simulator that encodes accurate individual behavior rules and produces simulated behaviors consistent with empirical observations, on both the individual and group levels. Critically, through multiple simulated experiments, our results highlight the value of individual sensitivity to site population in ensuring consensus. With the help of this social information, our model successfully reproduces experimental results showing the high cognitive capacity of colonies and their

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rational time investment during decision-making, and also predicts the pros and cons of social information with regard to the colonies' ability to avoid and repair splits. Additionally, we use the model to make new predictions about several unstudied aspects of emigration behavior. Our results indicate a more complex relationship between individual behavior and the speed/accuracy trade-off than previously appreciated. The model proved relatively weak at resolving colony divisions among multiple sites, suggesting either limits to the ants' ability to reach consensus, or an aspect of their behavior not captured in our model. It is our hope that these insights and predictions can inspire further research from both the biology and computer science community.

Keywords: Collective Behavior, Decision Making, Ant Colony

1 Animal groups are capable of remarkable displays of highly coordinated
2 behavior. Fish schools collectively choose foraging sites (Ward et al., 2012),
3 locusts self-organize into orderly swarms (Yates et al., 2009), oceanic fish
4 assemble in vast migratory shoals (Makris et al., 2009), and social insects
5 perform a host of collective actions including group foraging, construction of
6 complex nests, and adaptive allocation of tasks across the labor force (Char-
7 bonneau and Dornhaus, 2015; Detrain and Deneubourg, 2008; Detrain et al.,
8 2019; Oldroyd and Pratt, 2015; Perna and Theraulaz, 2017; Seeley, 1995).
9 How these group actions result from individual behavior remains a major
10 research challenge. Although well-informed leaders may play a role, group
11 organization is typically very decentralized (Detrain and Deneubourg, 2008;
12 Feinerman and Korman, 2017; Seeley, 1995). Coordination emerges from
13 interactions among large numbers of animals acting on limited local infor-
14 mation with appropriate decision rules. Connecting individual behavior to

group outcomes is too much for unaided intuition, hence mathematical models and agent-based simulations have become useful tools for understanding. In this paper, we present a model for a notable example of decentralized decision-making: nest site selection by ants of the genus *Temnothorax*.

Models, in combination with experimental studies, have already revealed much about these ants, making them a leading model system for collective decision-making (Pratt, 2019). Colonies live in pre-formed cavities such as rock crevices or hollow nuts; if their home is damaged, they are adept at finding candidate new homes, evaluating each site’s quality, and moving the entire colony to the best one. Their decision emerges from the separate efforts of many scouts, each independently recruiting nestmates to the site it has found. Because recruitment is quality-dependent, better sites accumulate ants more rapidly (Mallon et al., 2001). These differences are amplified by a quorum rule under which scouts accelerate recruitment to a site once its population crosses a threshold; the winner of the race to attain a quorum becomes the colony’s choice (Pratt et al., 2002). An agent-based model has shown that this algorithm helps the colony reach consensus on the best site (Pratt et al., 2005). Other models have shown how a colony can make a good choice even when no individual directly compares sites (Masuda et al., 2015a; Robinson et al., 2011), and how individual behavioral strategies optimize speed/accuracy tradeoffs at the colony level (Franks et al., 2013a; Marshall et al., 2006, 2009; Planqué et al., 2007; Pratt and Sumpter, 2006; Sumpter and Pratt, 2009).

Although successful, models of this process have been limited to the simple challenge of choosing between two distinct and equidistant nests in a con-

40 trolled laboratory environment. Real colonies face more complex scenarios,
 41 such as selecting among several sites of varying quality, avoiding splits when
 42 candidate nest sites are identical, and resolving colony splits when they occur
 43 (Doering and Pratt, 2019; Sasaki and Pratt, 2012). It also remains unclear
 44 how the colony maintains high performance with noisy and heterogeneous in-
 45 dividuals, and how individuals modify their behavior to account for changes
 46 in context or colony state. In addition, a large body of experimental work has
 47 uncovered new colony behavior that has yet to be explored in terms of how
 48 well our current understanding of the ants' collective algorithm can explain
 49 them. These include the more complex scenarios mentioned above, as well
 50 as effects on decision-making of colony size and emigration distance, colony
 51 reconnaissance of potential new homes, and the emergence of group-level ra-
 52 tionality despite individual-level irrationality (Franks et al., 2008; Sasaki and
 53 Pratt, 2011; Stroeymeyt et al., 2010).

54 To better capture the complexities of nest-site selection, we develop a
 55 new, flexible, general model for the analysis and exploration of the under-
 56 lying behavioral algorithms. We demonstrate the value of the model by
 57 reproducing the results of earlier models showing how the ants' algorithm
 58 can account for decision-making and speed/accuracy tradeoffs in simple two-
 59 choice experiments (Pratt and Sumpter, 2006; Pratt et al., 2005). We then
 60 extend the model to account for more recent empirical observations, includ-
 61 ing robust decision-making among larger option arrays and rational colony
 62 decisions about decision speed (Sasaki and Pratt, 2012; Sasaki et al., 2019).
 63 We also explore a proposed novel role for social information, in which ants
 64 directly incorporate nestmate presence into their assessment of nest site qual-

ity. We use the model to test the effect of such information on a colony’s ability to decide between two identical nests, a context that poses a particular challenge to consensus formation. Finally, we make predictions about the relationship between quorum size and the speed/accuracy tradeoff, and about the ability of a colony to re-unify after dispersal of its members among multiple competing sites.

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, an additional goal is to provide a versatile, easy-to-use and maintainable modeling tool that can be used to quantitatively test hypotheses beyond those included in this paper. From a theoretical perspective, our model can serve as a foundation for simpler models that allow rigorous proofs on convergence speed and accuracy.

The rest of the paper is organized as follows: Section 1 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 2 applies this framework, with designs and interpretations specific to the house hunting context. Section 3 describes our Python implementation of the house hunting simulator, instructions on running simulations, and their scoring goals and metrics. Section 4 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 confirmations of newly observed colony behaviors with limited experimental results, as listed in Section 5. Section 6 showcases simulation results that establish the power of the new social information rule in the

colonies’ ability to reach consensus. Next, Section 7 includes new predictions that await experimental test. Finally, Section 8 summarizes our results and proposes possible future research directions.

1. 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 2 we instantiate this language in the context of the house hunting process in ant colonies.

1.1. 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*.

- 113 • **action-types**, a set of the types of actions agents might perform. Each
114 element in the set is an *action-type*.
- 115 • **env-choices**, a set of values an agent can access in the environment.
116 Each element in the set is an *env-choice*.
- 117 • **actions**, a set of quadruples of the form $(\text{action-type}, \text{agent-id}, \text{agent-}$
118 $\text{id}', \text{env-choice}) \in \mathbf{action-types} \times \mathbf{agent-ids} \times \mathbf{agent-ids}' \times \mathbf{env-}$
119 $\mathbf{choices}$. Each element in the set is an *action*.
- 120 • **select-action**(*agent-id*, *state*, *env-state*, *all-external*): A *state* is a
121 pair of $(\text{external-state}, \text{internal-state}) \in \mathbf{external-states} \times \mathbf{internal-}$
122 $\mathbf{states}$. Each $(\text{agent-id}, \text{state}, \text{env-state}, \text{all-external})$ quadruple is
123 mapped to a probability distribution over the sample space of **actions**,
124 for which the second component is equal to the input argument *agent-id*
125 and the third component is not equal to it. The function then outputs
126 this probability distribution.
- 127 • **transition**(*agent-id*, *state*, *all-external*, *action*): A *state* is a pair of
128 $(\text{external-state}, \text{internal-state}) \in \mathbf{external-states} \times \mathbf{internal-states}$.
129 Each $(\text{agent-id}, \text{state}, \text{all-external}, \text{action})$ quadruple determines a *state*
130 as the resulting state of the agent identified by the input argument
131 *agent-id*. The function outputs the resulting *state*.

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

136 We define **all-externals** to be the set of all mappings from **agent-ids** to
137 **external-states**. Each element of the set is an *all-external* and represents a

138 particular mapping from **agent-ids** to **external-states** where each *agent-id*
139 is mapped to an *external-state*.

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

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

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

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

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

163 the resulting *state* of the transition.

164 1.2. Timing and Execution Model

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

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

175 Incorporating some theoretical ideas from (Ghaffari et al., 2015; Radeva,
176 2017), we divide the total time into *rounds*. Each round is a discrete time-
177 step, and times are the points between rounds. At any time t , there is a
178 corresponding system configuration t . The initial time is time 0, and the
179 first round is round 1, taking the system from configuration 0 at time 0 to
180 configuration 1 at time 1. In general, round t starts with system configuration
181 $(t - 1)$. During round t , agents can perform various **transition**'s, which take
182 the system from configuration $(t - 1)$ at time $(t - 1)$ to configuration t at
183 time t .

184 We now describe the execution of an arbitrary round t . At any point in
185 the execution of round t , each agent x is mapped to a *state*, *state_x*, which
186 is visible to agent x itself. However, to other agents, only agent x 's *external-*
187 *state*, *external_x* is visible. We denote *all-external* $\in$ **all-externals** to be the

188 mapping from every $agent-id \in \mathbf{agent-ids}$ to the corresponding $external-state$
 189 $\in \mathbf{external-states}$ in round t . These mappings can be updated during the
 190 execution.

191 Accounting for the randomness of the order of execution for all the agents,
 192 a randomly chosen permutation of $\mathbf{agent-ids}$ is generated at the beginning
 193 of round t , serving as the order of execution for the agents in the round. We
 194 also instantiate a set $Trans = \emptyset$ at the beginning of the round. An agent is
 195 prevented from changing its $state$ further in the round once it adds its $agent-$
 196 id to $Trans$, which can happen during its turn (even if there is no resulting
 197 state change) or when it performs a **transition** during another agent's turn.
 198 As a result, each agent can change its state at most once in the round. After
 199 all agents are in the set $Trans$, round t is over, and all agents enter round
 200 $t + 1$ synchronously.

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

205 Otherwise, agent x has not yet transitioned in round t . Let $state_x$ denote
 206 the $state$ of agent x . Agent x calls the function **select-action**($x, state_x, env-$
 207 $state, all-external$). The function outputs a probability distribution over the
 208 sample space of a subspace of **actions**, for which the second component is
 209 x , and the third component is not x . Agent x randomly selects an $action$,
 210 $act = (a, x, x', e)$, according to this probability distribution.

211 Agent x then calls **transition**($x, state_x, all-external, act$), to determine
 212 the resulting $state$, new_state_x , for agent x . As the initiating agent, x also

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

220 1.3. Discussion

221 Although our model keeps track of the *external-state* of all the agents
 222 in *all-external*, when performing a transition, an agent can only access *local*
 223 information in it. Locality here is flexible to the context, i.e. local to the
 224 location of the agent initiating an action.

225 Agent-based models are especially powerful for simulating and analyzing
 226 collective behaviors given their natural compatibility with object-oriented
 227 programming methodologies and their flexibility for allowing individual dif-
 228 ferences in realized state transition probabilities among the agents (De Vries
 229 and Biesmeijer, 1998; Sumpter et al., 2001; Masuda et al., 2015b; Pratt et al.,
 230 2005).

231 2. House Hunting Model

232 This section uses the framework defined in Section 1 to describe the house-
 233 hunting process.

234 2.1. Informal Description

235 An ant colony is composed of **adult workers** and brood items (imma-
236 ture ants), each group making up 40% to 60% of colony members. Adults
237 are roughly equally divided between active workers, who organize and exe-
238 cute emigrations, and passive workers, who, like brood items, are typically
239 transported to the new nest by active workers and not themselves recruit
240 nestmates (Pratt et al., 2005; Dornhaus et al., 2008; Valentini et al., 2020a).

241 There are four distinct phases for an active worker in the house-hunting
242 process. In the first, the **Exploration** phase, the ant randomly starts to
243 explore her surroundings for a suitable new nest. If she finds a candidate
244 site, she enters the **Assessment** phase, where she individually assesses the
245 site’s quality according to various metrics (Healey and Pratt, 2008; Franks
246 et al., 2003b; Pratt, 2005a). If she judges the site to be satisfactory, the ant
247 accepts it and enters the **Canvassing** phase, in which she returns to the
248 old nest to recruit other ants to the site by leading **forward tandem runs**
249 (FTR). In a FTR, the recruiter slowly leads a single follower (another active
250 worker) from the old nest to the new (Moglich, 1978; Richardson et al., 2007;
251 Valentini et al., 2020b). Upon arriving at the nest, the follower ant goes
252 directly into the Assessment phase and evaluates the nest’s quality indepen-
253 dently of the leader ant. If she finds the nest satisfactory, she will transition
254 to the Canvassing phase and start leading FTRs to the nest. A canvasser
255 continues leading FTRs until she perceives that the new nest’s population
256 has exceeded a threshold, or quorum (Pratt, 2005c). At this point, she en-
257 ters the **Transport** phase, in which she fully commits to the new nest as
258 the colony’s home. She ceases FTRs and instead switches to picking up and

259 carrying nestmates from the old to the new nest. These transports are faster
 260 than FTRs, and they are largely directed at the passive workers and brood
 261 items, hence they serve to quickly move the entire colony to the new nest
 262 (Pratt et al., 2002, 2005). Previous models and experiments indicate that the
 263 quorum rule helps the colony to reach consensus rather than splitting among
 264 multiple sites (Pratt et al., 2002; Franks et al., 2006, 2013b). Splitting be-
 265 comes a danger if ants at different sites, each ignorant of their nestmate’s
 266 discoveries, launch FTRs to their respective sites. The quorum rule makes it
 267 likely that whichever site first hits the threshold will quickly end up with all
 268 or most of the colony, due to the speediness of transport.

269 Although experimental evidence is equivocal, we assume that the quorum
 270 size is correlated with the number of adult workers in the colony (Dornhaus
 271 and Franks, 2006; Franks et al., 2006). We also assume that passive workers
 272 can contribute to quorum attainment. Once the quorum is met, the switch to
 273 Transport phase is irreversible: an ant continues transporting nestmates to
 274 her new home nest even if the nest population later drops below the quorum
 275 size (Pratt, 2005c). However, transporters do sometimes interrupt transport
 276 to search for and assess alternative nest sites. If the search yields a new site
 277 that is better than the ant’s current nest, then she exits the Transport phase
 278 and enters the Assessment phase with the new site as her candidate nest.

279 An ant in the Canvassing or Transport phase does not recruit indefinitely.
 280 Once the site from which she is recruiting is empty, she returns to her home
 281 nest and transitions back to the **Exploration** phase. However, this happens
 282 only upon meeting a “termination” condition consisting of ten occurrences
 283 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 (Pratt et al., 2002).

2.2. Formal Model

2.2.1. Model components

In this section, we show how each component in our modeling framework (Section 1.1) 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, 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

```

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.

1.1. Note that for consistency with our implementation in Section 3, we use -1 or an empty string “” to represent any invalid default integer or string values represented by $\perp$ in Section 1.

- **agent-ids**, the set containing all integers in the range $[0, \text{num_ants})$, where num_ants is the total number of ants in the colony. In addition, $\text{agent-ids}' = \text{agent-ids} \cup -1$. 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

323 - Exploration (searching for new nests), Assessment (assessing new
324 nests), Canvassing (leading other active workers on FTRs to her ac-
325 cepted candidate nest), and Transport (committing to the new nest
326 and rapidly carrying other ants to it). Note we abbreviate the four
327 phases to names “E”, “A”, “C” and “T”, respectively. The initializa-
328 tion of an *Ant*’s *phase* and *state_name* can be found in Section 2.2.3.
329 For each *phase*, the variable *state_name* take values from a different
330 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
```

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

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

- 346 [0, 10].
- 347 • **env-states**, a set of arrays, each being an array of the *Nest* class ob-
348 jects. Each array corresponds to an *env-state*. For an *env-state*, the
349 *Nest* at index 0 represents the original home nest and has *physical_quality*
350 0. All other *Nest*'s have *physical_quality* in range [0, 4]. The maxi-
351 mum quality 4 here is arbitrary. Recall that the array does not change
352 throughout the execution of the system, and the array is read from a
353 configuration file introduced in Section 3.1.
 - 354 • **action-types**, the set of the types of actions includes: “search”, “no_action”,
355 “find”, “follow_find”, “get_lost”, “reject”, “no_reject”, “accept”, “re-
356 cruit”, “quorum_met”, “quorum_not_met”, “stop_trans”, “delay”, “ter-
357 minate”, “lead”, “carry”. *Action-type* is initialized to “no_action”.
358 Each item in the set above is an *action-type*.
 - 359 • **env-choices**, the set of integers in $[0, \text{num_nests}) \cup -1$ where *num_nests*
360 is the number of nests in the environment. Each element in the set is
361 an *env-choice* and is an integer representing an index into *env-state*.
362 An *env-choice* has initial value -1.
 - 363 • **actions**, the same set as defined in Section 1.1. Note that not all
364 actions require a receiving agent, and not all actions require an *env-*
365 *choice*. In case that they are not needed, they take the invalid default
366 value -1.
 - 367 • **select-action**(*agent-id*, *state*, *env-state*, *all-external*): the same func-
368 tion as defined in Section 1.1. Refer to Section 2.2.2 for details.
 - 369 • **transition**(*agent-id*, *state*, *all-external*, *action*): the same function as
370 defined in Section 1.1. Refer to Section 2.2.3 for details.

371 2.2.2. The select-action function

372 The function **select-action**(x , $state_x$, env_state , $all_external$) outputs
 373 a probability distribution over the sample space of **actions**, for which the
 374 second component is equal to the input argument $agent_id$ and the third
 375 component is not equal to it. Let any $action$ in the sample space be denoted
 376 by (a, x, x', ec) , where the second component is fixed. We now list out the
 377 probability distribution on other components for each possible value of the
 378 $state_name$ variable in $state_x$, as it is the only variable in $state_x$ that affects
 379 the output probability distribution. The boldface words are parameters that
 380 we can tune and whose values are read from a configuration file, introduced
 381 in Section 3.1.

- 382 • For $search$, the probabilities of choosing a to be “find” and “no_action”
 383 are **search_find** and $1 - \text{search_find}$ respectively, and all other $action$ -
 384 $type$ ’s have 0 probability. Both variables x' and ec take the invalid
 385 default value -1 with probability 1.
- 386 • For $follow$, the probabilities of choosing a to be “follow_find” and
 387 “get_lost” are **follow_find** and $1 - \text{follow_find}$ respectively, and all other
 388 $action$ - $type$ ’s have 0 probability. Both variables x' and ec take the in-
 389 valid default value -1 with probability 1.
- 390 • For $reverse_lead$, the probabilities of choosing a to be “delay” and
 391 “no_action” are **transport** and $1 - \text{transport}$ respectively, and all other
 392 $action$ - $type$ ’s have 0 probability. Both variables x' and ec take the in-
 393 valid default value -1 with probability 1.
- 394 • For $quorum_sensing$, let the set $\tilde{X}$ be the set containing id’s of all
 395 agents with $external_state$ having $role \in \{0, 1\}$ and $location = state_x.location$.

396 If the set size $|\tilde{X}| \geq \text{quorum_threshold}$, the probabilities of choosing
397 a to be “quorum_met” and “quorum_not_met” are 1 and 0 respectively,
398 and are 0 and 1 otherwise, and all other *action-type*’s have 0 proba-
399 bility. Both variables x' and ec take the invalid default value -1 with
400 probability 1.

401 • For *lead_forward*, let $\tilde{X}$ be the set containing id’s of the agents that
402 are not x , and whose *external-state* has *role* = 0 and *location* =
403 *state.x.location*. The function selects an action $\widetilde{act} = (\tilde{a}, x, x', ec)$ ac-
404 cording to the following probability distribution. In case *terminate_count* <
405 10, $\tilde{a}$ is chosen among “lead” and “get_lost” with probabilities **lead_forward**
406 and **1-lead_forward** respectively, and all other *action-type*’s have prob-
407 ability 0. In case *terminate_count* $\geq$ 10, $\tilde{a}$ is “terminate” with prob-
408 ability 1. The variable ec is equal to $\{state.x.candidate_nest\}$ with
409 probability 1. The distribution of x' depends on $\tilde{a}$, as follows:

- 410 – For “lead”, if $\tilde{X} \neq \emptyset$, the variable x' is uniformly selected from
411 $\tilde{X}$, and all other values in *agent-id*’ have 0 probability; otherwise,
412 $x' = -1$ with probability 1.
- 413 – For “get_lost”, $x' = -1$ with probability 1.
- 414 – For “terminate”, $x' = -1$ with probability 1.

415 • For *transport*, let $\tilde{X}$ be the set containing id’s of all agents that are not
416 x , and whose *external-state* has *location* = *state.x.location*. In addi-
417 tion, let $\tilde{X}'$ be the subset of $\tilde{X}$ containing agents that have *role* $\in \{1, 2\}$.
418 The function first selects an action $\widetilde{act} = (\tilde{a}, x, x', ec)$ according to the
419 following probability distribution. In case *terminate_count* < 10, $\tilde{a}$ is
420 chosen among “carry” and “stop_trans” with probabilities **transport**

and **1-transport** respectively, and all other *action-types* 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 (Burns et al., 2016; Sasaki et al., 2015) and the nest population (Pratt, 2005d; Dornhaus and Franks, 2006). 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

446 pop (obtained from *all-external*) is

$$\frac{q}{4} + \mathbf{pop_coeff} \times \frac{pop}{num_ants}, \quad (1)$$

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

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

450 where λ is a parameter that controls how “steep” the sigmoidal function
451 is, and x is the above defined nest quality. Higher λ values correspond
452 to lower individual noise level, and bring $p(x)$ closer to a step function.

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

453

- 454 • For *arrive*, the probabilities of choosing a to be “reject” and “no.reject”
455 are $1 - p(x)$ and $p(x)$ respectively, where x is the difference in quality
456 of the candidate nest compared to the home nest (Equation 3) and
457 $p(x)$ defined in Equation 2. All other *action-type*’s have 0 probability.
458 The variable x' take the invalid default value -1 with probability 1.
459 The variable ec take the invalid default value -1 with probability 1.
460 To determine $p(x)$, an ant x is required to compare the quality of its

461 *candidate_nest* (with physical_quality q_1 and population pop_1) and its
 462 *home_nest* (with physical_quality q_0 and population pop_0). We still use
 463 the sigmoidal function in Equation 2, with the change that the input
 464 x to the function now is

$$\frac{q_1 - q_0}{4} + \mathbf{pop_coeff} \times \frac{pop_1 - pop_0}{num_ants} \quad (3)$$

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

467 2.2.3. The transition function

468 *Passive Workers and Brood Items.* Active worker scouts are defined as those
 469 who engage in the emigration process by independently discovering the new
 470 nests (entering without carrying or being carried) or by carrying brood items
 471 or other adult ants to the new nest or both. Passive workers remain in the
 472 old nest until they are carried to the new nest. Brood items are similar to
 473 passive workers but do not contribute to quorum attainment (Pratt et al.,
 474 2002; Dornhaus et al., 2008).

475 We use sn_p to denote a *state* with a certain *state_name* = sn and
 476 *phase* = p . Passive workers and brood items together form the passive ma-
 477 jority population in the colony. Their behavior pattern is thus very simple
 478 — they only have one *state_name*_{phase}, at_nest_E , available to them. They
 479 can only allow one *action* with *action-type* “carry” and themselves as the
 480 receiving agent. The action results in the *location* variable in their *state* set
 481 to the last component of the action, *env-choice*, and no other variables in
 482 their *state*’s can change throughout the execution. Therefore, the rest of the
 483 section focus on the *state* transitions of **active** workers only, including any

484 initiating and receiving ants involved.

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

490 We do not designate a separate “termination state” that disables an ant
491 from exploring further, but at the termination of the emigration process, we
492 expect most active workers to be in at_nest_E . This is enforced softly through
493 the population effect introduced in Section 2.2.2 - if an agent in at_nest_E
494 is in a nest with both a high physical quality and a high nest population it
495 is highly likely that she is happy staying put in this nest and stabilizes in
496 the state at_nest_E . As a result, the more agents stabilizes in the same nest,
497 the more likely that they will stay stable and that new agents will stabilize
498 as well. In the house hunting algorithm, the conditions that trigger this
499 “termination” behavior contains two cases, as mentioned in Section 2.1. The
500 details of this special “termination” case handling is discussed in the next
501 paragraph.

502 *Special and General Cases.* In the house-hunting algorithm, there are some
503 special cases that the **transition** function handles before outputting the re-
504 sulting *state*. To facilitate, we define a set **allowed-in**(*external-state*) to
505 be a mapping from **external-states** to subsets of **action-types**. Consider
506 an *external-state* s , and the allowed subset is then **allowed-in**(s), repre-
507 senting the set of actions the agent in the *external-state* s is allowed to
508 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) = $\emptyset$.

(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 2.1, the four distinct phases are in different boxes: Exploration, Assessment, Canvassing, and Transport.

We now list out how the function **transition**(*agent-id*, *state*, *all-external*,

(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 2.1, the four distinct phases are in different boxes - Exploration, Assessment, Canvassing, and Transport.

516 *action*) handles each of the special cases, and also the general case. Let the
 517 input argument *action* be expanded to the quadruple $(act = a, x, x', ec)$.
 518 Also recall that the set *Trans* is a set containing the id's of all the agents
 519 that have completed a *state* change in the round (Section 1.2).

- 520 • The first special case is if the input argument *agent-id* = x' . This case
 521 only happens when agent $x' \neq -1$ invokes (in agent x 's turn) a **tran-**
 522 **sition**($x', state, all\text{-}external, act$), where $state = (external', internal')$

is the current *state* of agent x' . If $x' \in Trans$ or if $a \notin \mathbf{allowed-in}(external')$, 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) $a \notin \mathbf{allowed-in}(external')$. 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

548 adds x to $Trans$, and ends its execution by outputting the original
549 input argument, $state$.

550 • Lastly, in the general case where none of the above special cases applies,
551 the function first adds x to $Trans$. Then it finds the black text box
552 corresponding to $state.phase$ and $state.state_name$ in Fig. 3b, and the
553 black text box that a leads to contains the $phase$ and $state_name$ of
554 the resulting $state$. The rest of the variables in $state$ are modified as
555 well, and the details are listed for each possible value of the ($phase$,
556 $state_name$) pair at the end of the section. The function then outputs
557 the resulting $state$.

558 In Fig. 3a and Fig. 3b, *action-type*'s are color-coded as shown in Table
559 1. We walk through in the supplement materials all possible transitions
560 of an ant and the associated changes in the internal and external states.
561 An example is an ant in at_nest_E has four possible actions. First, she can
562 perform “no.action” and remain in the current nest. Second, she can perform
563 “search” and go into the state $search_E$. Third, she can receive a “lead” by
564 another ant to follow a FTR to a destination nest, $ec \in \mathbf{env_choices}$, in
565 which case she sets $old_candidate_nest$ to the value of $candidate_nest$, and
566 sets $candidate_nest$ to ec . Then she transitions to the state $follow_E$. Finally,
567 she can receive a “carry” by another active worker ant to a destination nest
568 $ec \in \mathbf{env_choices}$, in which case her $location$ and $candidate_nest$ are changed
569 to ec , and she stays in at_nest_E .

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.

570 3. Model Simulation and Metrics

571 In this section we describe the configuration file that contains all the
572 parameters of the model in Section 2. We also quantitatively define the
573 speed and accuracy measures for our simulation runs. A detailed description
574 of the Python simulator implementation is in the supplemental material.

575 3.1. Configuration Parameters

576 There are three kinds of parameters: environment, algorithm, and set-
577 tings.

578 Environment parameters are controlled by the environment and not con-
579 sidered changable or tune-able. These include the number of ants in the
580 colony, and the number and physical qualities of the nests as potential new
581 nest options.

582 Algorithm parameters are parameters that we can manipulate in order to
583 change the *select-action* function and hence the outcomes of our simulations.
584 These include the λ for the sigmoid function in Equation 2, the pop_coeff
585 value, parameters related to quorum sizes, the probability of finding a new
586 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 2.2 and 2.2.2.

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

Baseline Default Parameter Values. Compared to the agent-based model in (Pratt et al., 2005), our model places less emphasis on assigning specific observed values to a large number of parameters, but rather on a simple and elegant model that is more agile in representing a wide range of possible behaviors. For that reason, some parameters cannot be directly drawn from existing empirical data. We estimate these parameter values in a trial-and-error fashion until simulation results match well with the empirical results in (Pratt et al., 2005). These baseline values are used as a default from Section 4 to 7, 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** $\times$ (num_active+num_passive) + **quorum_offset**) is observed to have a median value between 4 and 18 ants for worker populations from 24 to 150, with the quorum size having a signif-

612 icant positive correlation with the number of adult ants (Pratt et al., 2002;
613 Franks et al., 2015). Therefore, with a colony of 200 members (including 100
614 adult workers), we use a **quorum_thre** of 15% and set **quorum_offset** to
615 0, estimating a quorum size of 15. The value of **search_find** (range: 0 to
616 1) is determined experimentally by trial-and-error. This parameter can be
617 influenced by many other factors such as the spatial geometry of the nests
618 and the experience level of the individual. These nuances are not captured
619 in our model in the interest of simplicity. But they can significantly affect
620 the simulation outcomes, and are an important future extension of our work.
621 The parameter **follow_find** denotes the success rate of a tandem run without
622 the follower getting lost and starting a new search. A successful tandem run
623 requires that both ants reach the target nest. Empirical observations sug-
624 gest large variation in tandem success, with observed success ranging from
625 30% to over 90% (Pratt, 2008; Glaser and Grüter, 2018). However, even lost
626 followers enjoy a significantly increased chance of finding the target nest on
627 their own (Pratt, 2008). We thus chose a high FTR success rate of 0.9 to
628 capture both these direct and indirect effects of tandem following on nest
629 discovery. The parameter **lead_forward** (range: 0 to 1) is the probability
630 that an ant performs an FTR when in the *lead_forward* state. The alter-
631 native option, *get_lost*, is designed to model the slower speed of an FTR,
632 and is determined experimentally in a trial-and-error fashion. The param-
633 eter **transport** is the probability that an ant keeps transporting instead of
634 stopping to resume search for additional sites. The stopping probability is
635 observed to be between 0.06 and 0.44, meaning our **transport** should take
636 values between 0.56 and 0.94. We chose 0.7 as our baseline value.

Parameter	Value	Source
lambda_sigmoid	8	trial-and-error, Sec. 6.1
pop_coeff	0.35	trial-and-error, Sec. 6.1
quorum_thre	0.15	(Pratt et al., 2002; Franks et al., 2015)
quorum_offset	0	(Pratt et al., 2002)
search_find	0.005	trial-and-error
follow_find	0.9	(Glaser and Grüter, 2018; Pratt, 2008)
lead_forward	0.6	trial-and-error
transport	0.7	(Pratt et al., 2005)

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

637 An average colony size of 200 with 50 active workers, 50 passive workers,
638 and 100 brood items is within the range of real colony compositions (Franks
639 et al., 2015). One round approximately translates to 0.5-1 minutes, though
640 this is a very rough estimate. A simulation with 2000 rounds thus translates
641 to 16-32 hours, and one with 4000 rounds translates to 32-64 hours. The
642 values for variables **percent_conv** and **persist_rounds** are determined by
643 trial-and-error and rough estimates from past empirical observations.

644 3.2. Speed and Accuracy Measures

645 We define the speed and accuracy metrics below for the *whole emigration*
646 *process* until either convergence or the end of simulation, including cases
647 resulting in splitting.

648 *Convergence Score as Speed.* The final goal of the house hunting algorithm
649 is to achieve fast convergence in any given environment and stabilize at that

convergence. To assess how well this was achieved, we calculate a **convergence score** as the inverse of the round number when a persistent convergence started. If no persistent convergence was reached before the end of the simulation, the convergence score is 0. Each simulation run has a convergence score.

Accuracy. Another important metric is **accuracy**, which is defined for a group of simulation runs. This metric tells us how good the colony is at selecting the best choice in the environment. 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, has quality 0. The **accuracy** of the configuration is then

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

where p_i is nest i ’s convergence probability, and q_i is its normalized physical quality. If no convergence is reached (splitting), the physical quality corresponding to that probability will be 0, thus not contributing to the summation above.

4. Model Validation

We begin by validating our model against the same empirical data that were successfully accounted for by two earlier models (Pratt et al., 2005; Pratt and Sumpter, 2006). 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. All simulations for the rest of the paper default to the configuration file described in Section 3.1, unless specified otherwise.

4.1. *Single-Nest Emigrations*

The first question we ask is: does our model accurately reproduce 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 (Pratt et al., 2005). These include the number of recruitment acts per ant, the number of ants performing each recruitment type, and the number of ants arriving at the new site by different routes. We asked whether our model could replicate the empirical distributions. To answer the question, we simulated the single-nest experiments conducted in (Pratt et al., 2005), on the six colonies with compositions detailed in Table 3. We used default parameter values, except we increased *search_find* to 0.05. This increase accounts for the presence of only one new nest, hence all “find” actions after the first one are re-discoveries of this nest, which we assume has a higher probability than finding a previously unknown site (Pratt et al., 2005). In future work, this variable should be expanded to depend on other factors, such as the number of nests in the environment or the spatial geometry. We ran 500 simulations for each colony.

Colony	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 (Pratt et al., 2005).

696 *Results.* We compared the statistics of the model output to the same statis-
697 tics reported in (Pratt et al., 2005) (Fig. 4). Fig. 4(a) shows the histograms
698 of individual workers grouped by the number of recruitment acts. More than
699 half of the simulated workers never recruited, consistent with the empirical
700 finding of about 60% non-recruiting active workers. The other bins show
701 similar mean and variance to the empirical data. Fig. 4(b) classifies ants
702 by their recruitment behavior, and the breakdowns are again consistent with
703 the experimental observations. Fig. 4(c) categorizes workers by their routes
704 to discovery of the candidate nest, and is again consistent with the find-
705 ings in (Pratt et al., 2005), at least when the experimental data are pooled
706 over six emigrations by three colonies. However, the distributions across the
707 three different routes vary strongly across emigrations. Indeed, the results
708 in (Pratt et al., 2005) notably differ from those in (Pratt, 2005b). While
709 our model does not account for this variation, we conclude that it does ad-
710 equately reproduce key distributions in recruitment behavior in single-nest

711 emigrations.

712 4.2. Two Unequal Nest: Splits

713 The second question we ask is: does our model account for the degree
714 of splitting in two-nest emigrations with unequal qualities? In these circum-
715 stances, colonies do not always make a unanimous choice, but may temporar-
716 ily split between the sites before eventually coalescing on a single one. We
717 focus on splitting because it is a primary hindrance to consensus. We mea-
718 sure splitting as the percentage of brood items in the better candidate nest
719 at the time when the last ant has been moved from the home nest.

720 We replicated the two-nest emigrations in (Pratt et al., 2005), with six
721 colonies whose member compositions are listed in Table 3. We set **nest_qualities**
722 = [0,1,2], representing a destroyed old nest and two candidate nests of mediocre
723 and good quality, respectively. The rest of the configuration parameters were
724 left at the default values.

725 We ran 500 simulations for each colony, and for each colony we recorded
726 the average percentage of brood items in the better nest at the time the
727 home nest became empty. To compare the simulations with empirical data,
728 we measured for each colony the proportion of simulations departing as far
729 or farther from the colony average as did the experimental value. Twice this
730 proportion gave the p-value for a test of the null hypothesis that the observed
731 value was drawn from the same probability distribution as the simulated
732 values.

733 *Results.* The results show no significant difference between experiment and
734 simulation for five of six colonies (Table 4). This outcome validates our

Figure 4: (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. Blue bars are results from (Pratt et al., 2005). Orange bars show our simulation results. Bar values are averaged over 500 simulations. Error bars show standard deviations.

Colony	% Pred	%Observed	P
A4	59 $\pm$ 17	61	0.86
A6	61 $\pm$ 28	80	0.56
A8	63 $\pm$ 30	99	0.36
A14	59 $\pm$ 20	98	0.1
A16	61 $\pm$ 34	100	0.5
A17	60 $\pm$ 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.

735 model’s ability to reproduce observed patterns of splitting in two-nest emi-
736 grations for a variety of colony compositions.

737 4.3. Two Unequal Nests: Speed-Accuracy Trade-off

738 The third question we ask is: does our model reflect the way that colonies
739 trade off speed and accuracy when the urgency of the emigration changes?
740 In “urgent” situations, ants face a critical need for immediate new shelter
741 and thus benefit from moving out of the old nest location as fast as possible.
742 In contrast, in less urgent situations they can deliberate longer among alter-
743 natives to increase the likelihood of moving directly to the best site (Pratt
744 and Sumpter, 2006; Dornhaus et al., 2004). We simulated experiments that
745 adjusted urgency by offering colonies a choice between a mediocre and a good
746 nest under two circumstances: their old nest has just been destroyed (high
747 urgency) or their old nest is of acceptable quality but worse than either of
748 the new candidates (low urgency). Our simulations followed the same tactic

by tuning the physical quality of the home nest to adjust urgency. 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 was set to 16 in order to increase the ants' sensitivity to home nest quality differences, and **pop_coeff**, which was set to 0 in order to better match the model assumptions in (Pratt and Sumpter, 2006). As in (Pratt and Sumpter, 2006), we measured the duration of emigration as the time in rounds at which the old site was completely abandoned, and we measured 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 taken to complete an emigration decreased as urgency increased (i.e., as old nest quality decreased) (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 (Pratt and Sumpter, 2006).

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 the existence of other mechanisms at work that this simulation failed to capture. One such mechanism could be sensitivity to the presence of nestmates when assessing the quality of a nest. This could enhance consensus by amplifying

the differential treatment of competing nests, as the better one's population increases and makes it still more attractive. Our model can capture this phenomenon by using a non-zero pop_coeff , a possibility explored further in the next section.

Figure 5: (a): From (Pratt and Sumpter, 2006): Speed and accuracy of decision-making in high-urgency and low-urgency 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, under high urgency (blue bars) and low urgency (yellow bars). (b): Simulation results for high and low urgency emigrations. Top and bottom panels correspond to those in (a). Simulations were run for more urgency levels than in the experiments.

5. Confirmation of New Experiments

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. Section 5.1 examines a colony’s ability to choose well when faced with larger option arrays; and Section 5.2 focuses on how colonies make rational decision time investments depending on nest quality differences.

Figure 6: The proportions of colonies that eventually moved into poor or good nests. (a): Empirical results in 2-nest and 8-nest settings (Sasaki and Pratt, 2012). (b): Simulation results from our model in 2-nest, 8-nest, and 14 nest settings.

5.1. Colonies Have High Cognitive Capacity

How well do colonies perform when selecting from many nests? A previous study (Sasaki and Pratt, 2012) showed that colonies are quite good at selecting a single good nest from a set of eight nests, four of which are good and four of which are mediocre. This is in contrast to individual ants, who are as likely to choose a mediocre as a good nest when faced with the same scenario. The colony advantage has been hypothesized to result from sharing the burden of nest assessment: very few of the scouts ever visit more than

one or two nests, whereas a lone ant visits several, potentially overwhelming her ability to process information about them successfully. We simulate this experiment to determine whether we can reproduce both the colony’s ability and the observed distribution of nest visits across scouts.

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

Results. First, we found that simulated colonies reached consensus on a good nest with high probability, matching that seen in empirical data (Fig. 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. The proportion of ants visiting only one or two nest was similar in the simulations and experiments (Sasaki and Pratt, 2012): over 80% of individual ants visited only one or two nests in the course of the emigration. Fig. 7 shows similar pattern is seen for the number of transports: that is, if we focus only on the ants who contributed to the emigration by transporting nestmates, over 80% visited only one or two nests. Thus, ants that access many nests have a minor role in the transportation process, supporting the hypothesis that colonies’ high cognitive capacity results from avoiding the overloading of individual ants.

Figure 7: Proportions of transport efforts as a function of the number of candidate sites visited by each ant. The blue bars show the percentage of transports done by ants that visited a given number of nests (Sasaki and Pratt, 2012), and the dark orange bars show the same for simulated ants. Colonies choose among eight nests (four good and four mediocre) in both simulations and experiments (Sasaki and Pratt, 2012).

817 5.2. Colonies Make Rational Choices about Decision Speed

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

826 We simulate this scenario to determine if we can reproduce the same
827 pattern, but we also explore a broader range of quality differences to bet-
828 ter describe the relation between quality difference and decision time. We
829 designed an environment with two candidate nests, one good and the other

mediocre. The good nest has physical_quality 2 in all simulations, but the physical_quality of the mediocre nest varies across simulations from 0.2 to 1.7. We asked whether the quality of the mediocre nest is correlated with the convergence score (a measure of decision speed). We ran 300 simulations for each environment with a colony of size 200, consisting of 50 active workers, 50 passive workers, and 100 brood items. We repeated this set of simulations for five different values of **lambda_sigmoid** values: [8,10,12,14,16].

Results. If our model reproduces the rational time investment choices of colonies (Sasaki et al., 2019), then we expect the convergence score to increase as the mediocre nest quality increases, thus becoming more similar to the good nest. Our results partially match this prediction, with convergence score increasing as the mediocre nest quality goes from 0.2 to about 1 (Fig. 8). However, at higher mediocre nest qualities, the pattern reverses and convergence score declines. This basic pattern is seen for all tested values of **lambda_sigmoid**.

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

Why might this happen? Recent studies have explained the behavioral difference between individuals and colonies via two different decision models: the tug-of-war model describes individual behavior, while colony behavior is better accounted for by the horse race model (Kacelnik et al., 2011). The tug-of-war correctly predicts the irrational behavior of individual ants, in

855 that their decision-making slows down for options that are more similar.
856 The horse race, in contrast, correctly predicts colonies' rational acceleration
857 of decision making for similar options. We hypothesize that the applicability
858 of these models to the colony's behavior changes as the quality difference
859 changes. More specifically in Fig. 8, before the peak score is reached, the
860 colony may effectively distribute its decision-making across many ants with
861 limited information, the situation envisioned in the horse-race model. After
862 the peak score is reached, the colony may come to depend more on individ-
863 ual comparisons between nest sites made by a few well-informed ants, and
864 thus to show the irrational slow-down predicted by the tug-of-war model.
865 It could also be the case that more transports are performed between the
866 two candidate nests as the likelihood of the mediocre nest achieving quorum
867 attainment increases.

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.

868 6. The Power of Social Information

869 In this section, we explore the influence of social information on migration
 870 speed, accuracy, and cohesion. Section 6.1 explores correlations between
 871 **pop_coeff** and the degree of randomness in individual decision-making; and
 872 Section 6.2 reveals how **pop_coeff** decreases splitting by colonies facing two
 873 equal options.

874 6.1. Balancing Personal and Social Information

875 Individual ants are capable of directly comparing nests and choosing the
 876 better one, but their discriminatory ability is less than that of whole colonies.
 877 This may be seen as a kind of “wisdom of crowds,” in which the estimations of
 878 many noisy individuals are integrated into a more precise group perception.
 879 Ants do this via positive feedback loops based on recruitment, which can
 880 amplify small differences in site quality (Sasaki et al., 2013). They also
 881 use social information via the quorum rule, under which full commitment
 882 to a site is conditioned on a minimum number of nestmates “voting” for it
 883 by spending time there. The quorum rule inspired us to consider another
 884 way that ants might use social information to improve decision-making: by
 885 taking population into account when assessing a site’s quality. We do this via
 886 the parameter **pop_coeff**, which controls the degree to which the presence of
 887 nestmates increases a site’s perceived value. We propose that this population
 888 sensitivity might be able to complement the noisy perception of individual
 889 ants, modeled by the parameter λ in the Eq. 2. We hypothesize that ants
 890 may adapt to different values of **lambda_sigmoid** by changing the value
 891 of **pop_coeff**. In particular, we sought evidence for a correlation between

the values of **lambda_sigmoid** and **pop_coeff** needed to achieve the best convergence score.

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

Results. The results show evidence for an inverse relation between **pop_coeff** and **lambda_sigmoid** (Fig. 9). For each value of **lambda_sigmoid** in the range [2,16], there is a value of **pop_coeff** that maximizes the convergence score, and this value increases as **lambda_sigmoid** decreases. Thus, when an individual ant makes noisy local decisions (modeled with lower values of **lambda_sigmoid**), she can counteract this deficiency by relying more on the input of her peers through a higher value of **pop_coeff**.

However, a high value also has risks. Here we interpret the advantages and disadvantages of *increasing* the value of **pop_coeff**:

Advantages.

- Higher momentum in the system. This can promote the colony to accumulate population at a certain nest more quickly, and thus achieve faster convergence.
- Better prevention of splits. Multiple candidate nests may reach the quorum, especially when the nests have similar physical qualities. This can lead to the colony splitting between more than one site. 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”.

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

These trade-offs suggest that there is an optimal value of **pop_coeff** for a given **lambda_sigmoid** as seen in Fig. 9. This predicts that colonies may

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

931 *6.2. Avoiding Splits Between Two Equal Nests*

932 In this section we further explore how social information can help colonies
933 to reach consensus when faced with two identical nests. Many social insects
934 have highly nonlinear recruitment mechanisms that lead to symmetry break-
935 ing when faced with two identical resources. For example, ant species that
936 recruit via trail pheromones will choose one of two identical food sources
937 rather than forming trails to both. This is because the attractiveness of a
938 trail is a sigmoidal function of the amount of pheromone it contains, which
939 leads to rapid amplification of small random differences in the strengths of
940 competing trails (Beckers et al., 1990; Perna et al., 2012). However, simi-
941 lar experiments on *Temnothorax* ants found that they do not always break
942 symmetry, instead exploiting both feeders equally, a result that has been
943 attributed to the linear relationship between tandem running effort and re-
944 cruitment success (Shaffer et al., 2013).

945 An open question is whether this lack of symmetry breaking also holds for
946 nest site selection. When presented with identical nests, do colonies choose
947 only one or split between them? If they can reach consensus, then how
948 do they do so? One possibility is that the quorum rule provides sufficient
949 non-linearity to amplify small random differences in site population, thus
950 ensuring that the colony does not split. Another possibility is that colonies
951 have some other as of now unrecognized mechanism of avoiding splits. A
952 good candidate for such a mechanism is incorporation of site population into
953 each scout’s assessment of site quality, as discussed in Section 6.1. This would

allow amplification of early random differences in population, by increasing the likelihood of recruitment to the nest with more ants. We explore this question by simulating emigrations in which a colony is presented with two identical nest sites. We assess how well they reach consensus on a single one. We also vary the degree of scout sensitivity to site population by considering different values of **pop_coeff**.

Figure 10: Simulation results for colonies choosing between two identical nests. The histograms show the distribution of the percentage of the colony occupying the left nest, for three different values of **pop_coeff**.

We ran 200 simulations each for **pop_coeff** = [0, 0.1, 0.2, 0.3, 0.4], in an environment with **nest_qualities** = [0,2,2]. We set **lambda_sigmoid** to 16 in order to be more sensitive to temporal differences in nest populations. From an initial set of simulations, we observed that almost all simulations converged within the default value of **num_rounds**. Therefore, in order to gain more insight into the effect of **pop_coeff** on the degree of splitting before convergence, we set it to a smaller value 1000. The rest of the parameters take the default values.

968 *Results.* The simulation results show strong symmetry breaking (Fig. 10).
 969 That is, a large majority of simulations ended with 80% to 100% of the colony
 970 in one of the two nests. When consensus was reached, it was roughly equally
 971 likely to be in nest 1 or nest 2, producing the distinctive U-shaped distribution
 972 seen in Fig. 10. This pattern was true regardless of the value of **pop_coeff**,
 973 suggesting that the quorum rule is enough to generate symmetry breaking in
 974 this case. However, as the value of **pop_coeff** increases, the histograms also
 975 aggregate more towards the two end bins, meaning there are fewer split cases.
 976 Thus we confirm the positive effect of **pop_coeff** in reducing splits, either
 977 by prevention or by facilitating later re-unification. These mechanisms can
 978 have significant effects in more challenging environments with more candidate
 979 nests.

980 7. New Predictions

981 We also use our model to develop new hypotheses and predictions for
 982 future experimental study. Section 7.1 gives simulated evidence for a sur-
 983 prising speed-accuracy trade-off for the entire emigration process, tuned by
 984 the quorum size; and Section 7.2 discusses colony re-unification after splits
 985 with an increasing level of difficulty.

986 7.1. Quorum Size and the Speed/Accuracy Trade-off

987 *Temnothorax* colonies can adjust their behavior to adaptively trade off the
 988 speed and accuracy of decision-making (Pratt and Sumpter, 2006; Dornhaus
 989 et al., 2004) (Section 4.3). One of the behavioral tools implicated in this
 990 adjustment is the quorum rule. Colonies lower the quorum in more urgent
 991 situations, increasing their reliance on individual judgement. This allows

992 them to make rapid decisions and quickly move the colony out of the old nest,
993 at the cost of an increased probability of splitting or choosing an inferior nest
994 (Franks et al., 2003a, 2009).

995 When considering speed, previous studies focused on the time to move out
996 of the old nest, but the completion of an emigration often requires more than
997 that. A fast “first” decision does not always mean a fast emigration. In fact, a
998 low quorum and hence a fast “first” decision could lead to slower emigrations
999 (Franks et al., 2009) since it could cause more splitting, which the colony must
1000 subsequently resolve in a second phase of movement. Here, we explore the
1001 effect of quorum size on the speed and accuracy as we have defined them for
1002 the whole process (Section 3.2). Within the accuracy measure, we pay special
1003 attention to the rate of splitting, which is the percentage of emigrations that
1004 do not reach a persistent convergence within the given number of rounds.
1005 A natural question arises: is there a speed-accuracy trade-off if we define
1006 “speed” as (the inverse of) the time taken to the final completion of the
1007 emigration? In other words, do the convergence score and accuracy have
1008 inverse correlations with **quorum_thre**, and are these relationships affected
1009 by splitting rate?

1010 We simulated an environment with candidate nests [0.5, 1, 1.5, 2] and a
1011 home nest with quality 0 as usual. We used a colony of size 200, consisting
1012 of 50 active workers, 50 passive workers, and 100 brood items. Quorum size
1013 is assumed to be proportional to the total number of adults in the colony,
1014 and is set to **quorum_thre** $\times$ **num_adults**. We varied **quorum_thre** from
1015 0.03 to 0.39, and set **pop_coeff** to either 0 or 0.35. We set *num_rounds* to
1016 2000 and ran 100 simulations for each unique combination of **quorum_thre**

1017 and **pop_coeff**.

Figure 11: (a), (b): Convergence score and Accuracy as a function of **quorum_thre**, with **pop_coeff** = 0 and 0.35 respectively. (c), (d): Probabilities of converging to each nest (or splitting) as a function of **quorum_thre**, with **pop_coeff** = 0 and 0.35 respectively.

1018 *Results.* The simulation results show that the convergence score generally
1019 has a reverse-U shape that peaks at **quorum_thre** = 0.24-0.27 (Fig. 11a,
1020 Fig. 11b). In addition, the accuracy measure has a similar shape, but peaks
1021 roughly at **quorum_thre** = 0.1-0.15. The split rate, in contrast, has a U-
1022 shape, with a trough around **quorum_thre** = 0.15 to 0.18 (Fig. 11c and
1023 11d).

1024 The above results indicate a surprising speed-accuracy trade-off in the
 1025 segments where the two lines form an “X” shape in Fig. 11(a) and (b): the
 1026 increase of **quorum.thre** is accompanied by a decrease in accuracy and an
 1027 increase in speed. This is the opposite of our findings in Section 4.3 and in
 1028 the related experimental work (Pratt and Sumpter, 2006; Dornhaus et al.,
 1029 2004). However, it is important to note that the current definitions of speed
 1030 and accuracy differ from those used in the prior work, which defined both
 1031 quantities only up to the point where the old nest is empty. The results
 1032 on splitting rate could give more insight into the conflicting results - if re-
 1033 pairing splits is costly, lowering the probability of splits by increasing the
 1034 quorum would indeed significantly increase the average convergence score.
 1035 But another factor is that setting the quorum too high to reach will also de-
 1036 lay convergence. These results point to the need for better understanding of
 1037 how colonies reunite after splits, as well as the costs of reunification relative
 1038 to other components of the emigration.

1039 7.2. Reunification after Splitting

1040 Finally, we touch on another aspect of the robustness of the house hunt-
 1041 ing algorithm — reunification after splitting. Experimental studies on the
 1042 speed-accuracy trade-off showed that colonies often split in urgent emigra-
 1043 tions, but they also noted that split colonies were eventually able to reunite
 1044 (Franks et al., 2003a, 2009). Later studies (Doering and Pratt, 2019, 2016;
 1045 Doering et al., 2020) showed that artificially divided colonies readily re-unite,
 1046 using the same behavioral tools as in emigrations, but relying more on the
 1047 efforts of a small group of active workers. These findings suggest that emi-
 1048 grations depend on a mixture of individual and colony-level decision making.

Figure 12: Convergence scores and splitting for environments with different numbers and qualities of nests. (a) Convergence score and accuracy as a function of the number of nests with quality 1 in the environment. (b) Convergence score and accuracy as a function of the number of nests with quality 2 in the environment. (c), (d) Same environments as (a) and (b), respectively, but plotting convergence probabilities to different nests (or splitting) on the y-axis.

In this section, we explore how well our model achieves convergence after an arbitrary division among multiple nests. What can we learn about the mechanisms that achieve re-unification?

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

were of quality 1, and another set in which one nest was of quality 1 and the rest were of quality 2. We ran 300 simulations for each environment with a colony of size 200, consisting of 50 active workers, 50 passive workers, and 100 brood items.

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

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

8. Discussion

In this paper, we introduce an agent-based modeling framework that can be used to formally represent a variety of distributed algorithms used by animal groups to understand the emergence of collective intelligence. We used the framework to examine the collective nest site selection process in colonies of *Temnothorax* ants. To test against existing experimental data and to make predictions, we built a convenient Python simulator that can easily be extended to add extra features. Our model reveals several underlying mechanisms behind the flexible, noise-tolerant and efficient collective house-hunting process in ant colonies. These include the mixed applicability of the horse-race model and the tug-of-war model to the house-hunting case; the colony's emergent ability to tolerate noise and prevent splits by balancing social information and personal information; and the impact of splitting on the speed-accuracy trade-off of the emigration. Moreover, the generalizable modeling framework that we present can be used to investigate many other collective behaviors in biological systems.

The model successfully replicated published colony-level outcomes, suggesting that it accurately accounts for underlying individual behavior. It performed as well as an earlier model (Pratt et al., 2005), but did so with a more concise and elegant set of individual decision rules. The new model was also able to replicate more realistic and challenging emigration contexts that have not previously been modeled. Thus, on top of matching previous studies of simple one- and two- choice environments, our model successfully and quantitatively predicts colony behavior in environments with many more choices. Additionally, with varying degrees of experimental support, our model makes

speculations on the quantitative relationships between multiple parameters and their effects on the colony's collective behavior. The most important highlight is a novel role of social information in the speed, accuracy, and the rate of splitting during emigrations. The model and the accompanying software are versatile and easy to extend to additional investigations on unexplored scenarios such as emigrations in a changing environment. However, modeled colonies proved relatively weak at resolving splits in more challenging environments (i.e., with the colony split among several similar high-quality sites). This may reflect real limitations of the ants' algorithm, but it seems more likely that the model underestimates their reunification abilities. This topic has so far received little attention; further development of this model could help to guide new experimental work.

In the rest of this section, we discuss several specific directions for future research. While our model captures many aspects of individual behavior, it leaves out some important features, including many that affect timing. These include 1) effects of the spatial distribution of nests, 2) effects of individual experience on recruitment probability and speed, and 3) actions that may last a variable duration such as the evaluation of a new nest. Adding these to the model would allow it to explore a broader range of colony abilities and to reveal as yet unknown components of individual behavior and how they interact with known aspects. For example, more realistic models of timing would undoubtedly affect the discovery behavior currently captured by the single variable *search_find*.

On the model analysis side, there are many directions for further research. First, we note the link between the effects of different quorum sizes and the

1131 horse-race and tug-of-war models that have been successfully used to describe
 1132 group and individual decision-making, respectively, in these ants (Kacelnik
 1133 et al., 2011). Our model finds that group decision-making may be better cap-
 1134 tured by the tug-of-war model when a colony is choosing between two very
 1135 similar options. If so, this suggests that colonies can change their relative re-
 1136 liance on individual decision-making according to the decision context. This
 1137 indicates the value of developing a more quantitative model that combines
 1138 the tug-of-war and the horse-race models, based on the same factors that
 1139 affect how a colony chooses the most beneficial quorum size.

1140 Additionally, our model shows the potential utility of individual ants
 1141 taking account of site population when assessing a site’s quality. Whether
 1142 real ants use social information in this way has not yet been experimentally
 1143 tested. Our results suggest that it may be important for preventing and
 1144 repairing split decisions. However, the amount of social information that
 1145 individuals should rely on is an intricate balance, as we described in Section
 1146 6.1. It would be highly valuable to quantify the relationship between the
 1147 frequency and degree of splitting to the quorum size and to **pop-coeff**. A
 1148 related research direction is to find out other factors that allow colonies to
 1149 robustly reunify in split cases. However, the runtime of our program over
 1150 hundreds of simulations can be significant, making it difficult to investigate
 1151 the system dynamics and performance in all possible parameter settings.
 1152 Overcoming this challenge requires software optimization techniques such as
 1153 code parallelization and possibly further model simplifications.

1154 On the theoretical analysis side, our model serves as a stepping stone for
 1155 more rigorous mathematical formulations and proofs of guaranteed bounds

on any metrics of interest. Starting with simpler environments, our model can be reduced to analytically derive the goals different mechanisms can and cannot achieve. These results can then potentially provide insights on why certain collective behaviors have emerged through evolution, as well as on engineering artificial distributed systems subject to similar limitations to reach consensus.

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

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1370 10. Supplemental Materials

1371 10.1. State Transition Details

1372 *Exploration.*

- 1373 • An ant in at_nest_E has four possible actions. First, she can perform
1374 “no_action” and remain in the current nest. Second, she can perform
1375 “search” and go into the state $search_E$. Third, she can receive a

1376 “lead” by another ant to follow a FTR to a destination nest, $ec \in$
1377 **env-choices**, in which case she sets *old_candidate_nest* to the value of
1378 *candidate_nest*, and sets *candidate_nest* to ec . Then she transitions to
1379 the state *follow_E*. Finally, she can receive a “carry” by another ac-
1380 tive worker ant to a destination nest $ec \in$ **env-choices**, in which case
1381 her *location* and *candidate_nest* are changed to ec , and she stays in
1382 *at_nest_E*.

- 1383 • An ant is in the state *follow_E* if she is in the middle of following an
1384 FTR, and has two possible actions. First, she can successfully follow
1385 the FTR to the destination nest (“follow_find”) and change her *location*
1386 to her *candidate_nest*, which results in the state *arrive_E*. Otherwise,
1387 she may lose contact with her tandem leader (“get_lost”), and then
1388 enters the state *search_E* and assigns the value of *old_candidate_nest* to
1389 *candidate_nest*.
- 1390 • An ant in the state *search_E* has three possible actions. First, she
1391 can have “no_action” and transition to *at_nest_E* by staying at her last
1392 known *location*. Second, she can “find” a new nest, $ec \in$ **env-choices**,
1393 in this round, assign the value of *candidate_nest* to *old_candidate_nest*
1394 and assign ec to both *location* and *candidate_nest*, and transition into
1395 *arrive_E* state to evaluate it further. Third, she can receive an action,
1396 “carry”, and the results are the same as receiving the “carry” action in
1397 *at_nest_E*.
- 1398 • An ant in the state *arrive_E* has two action options. First, she can
1399 “reject” the nest she just arrived at. She then assigns the value of
1400 *candidate_nest* to *location* and then that of *old_candidate_nest* to *candidate_nest*

1401 go into the $search_E$ state. Otherwise, if she performs “no_reject”, she
1402 transitions into the state at_nest_A and assigns the value of $candidate_nest$
1403 to $location$.

1404 *Assessment.*

- 1405 • An ant in the state at_nest_A is assessing a new nest and is currently
1406 located at that nest. From here, three actions are available. First, she
1407 can “accept” the nest if she deems it high quality, which results in her
1408 transitioning to at_nest_C . Second, she may perform “search” to get into
1409 the $search_A$ state. Third, she can receive a “lead” by another ant to
1410 follow a FTR to a destination nest, in which case she assigns the value
1411 of $candidate_nest$ to $old_candidate_nest$ and assigns the destination
1412 nest $ec \in \mathbf{env_choices}$ to $candidate_nest$, and then she transitions to
1413 the state $follow_A$. Finally, she can receive a “carry” by another active
1414 worker ant to a destination nest $ec \in \mathbf{env_choices}$, in which case her
1415 $location$ and $candidate_nest$ are changed to ec and transitions back to
1416 at_nest_E .
- 1417 • An ant in the states $follow_A$ or $search_A$ has the same options and vari-
1418 able changes as in $follow_E$ or $search_E$ respectively, but the resulting
1419 state sub-scripted with A except the “carry” action.
- 1420 • An ant in $arrive_A$ state has the same options and variable changes as
1421 in $arrive_E$, but with “reject” action leading to $search_C$.

1422 *Canvassing.*

- 1423 • An ant in at_nest_C state has three available actions. First, she can
1424 decide to “recruit” and go into $quorum_sensing_C$ state. Second, she
1425 can decide to “search” more and result in $search_C$ state. Third, she

1426 may receive a “carry” by another active worker ant to a destination
1427 nest, in which case her *location* and *candidate_nest* are changed to
1428 that nest and results back to *at_nest_E*.

1429 • An ant in *quorum_sensing_C* state is at a nest different than her home
1430 nest, and has two options. If she estimates the current nest population
1431 to be higher than the quorum threshold, she performs “quorum_met”,
1432 swap the values of *home_nest* and *candidate_nest*, and enters the state
1433 *transport_T*. Otherwise, she performs “quorum_not_met” and enters
1434 *lead_forward_C* state.

1435 • An ant in *lead_forward_C* state has three actions available to her. First,
1436 she can “lead” another active worker and lead her on an FTR from the
1437 original home nest to the candidate new nest. She changes her *location*
1438 to the value of *candidate_nest*, and enters *at_nest_C* state. Second, she
1439 can “get_lost” in the process if she loses contact with the follower,
1440 and enters *search_C* state. Lastly, she can “terminate” her emigra-
1441 tion if the termination conditions are met, namely if she has repeated
1442 attempts to call other active workers who are also in *lead_forward_C*
1443 state. In this case, she changes her *location* to her *home_nest*, resets
1444 *terminate_count* to 0, and enters state *at_nest_E*.

1445 • An ant in *search_C* state has the same options and variable changes as
1446 in *search_E* with the resulting state sub-scripted with *C*.

1447 • An ant in *arrive_C* state has the same options and variable changes as
1448 in *arrive_E*, but with “reject” action leading to *search_C*.

1449 *Transport.*

1450 • An ant in *at_nest_T* state has the same options and variable changes

- 1451 as in at_nest_C with the resulting state sub-scripted with T , except
 1452 that a “recruit” action results in $transport_T$, and that it can receive
 1453 one additional action “lead”, in which case she assigns the value of
 1454 $candidate_nest$ to $old_candidate_nest$, assigns the destination nest $ec \in$
 1455 **env-choices** to $candidate_nest$, and transitions to $follow_T$.
- 1456 • An ant in $transport_T$ state has three available actions. First, she can
 1457 decide to carry another ant, active, passive, or brood, to her newly com-
 1458 mitted nest. This results in her entering $reverse_lead_T$ mode, meaning
 1459 she can lead a reverse tandem run (RTR). These are tandem runs lead
 1460 from the newly committed nest to the old home nest or another nest.
 1461 Second, she can decide to “stop_trans” and stops her transport to go
 1462 into the state $search_T$. Third, similar to the state $lead_forward_C$,
 1463 there is a “terminate” action when the termination condition is met,
 1464 namely if she has repeated attempts to carry other active workers who
 1465 are also in $transport_T$ state. In this case, she changes her *location* to
 1466 her *home_nest*, resets *terminate_count* to 0, and enters state at_nest_E .
 - 1467 • An ant in $reverse_lead_T$ only has two actions as her options. First, she
 1468 may perform *no_action* and returns to at_nest_T state. Second, she may
 1469 experience “delay” in her tandem runs, and will stay in $reverse_lead_T$
 1470 state. There’s no conclusion on the purpose of RTRs at this point in
 1471 the research community, so we model it as a round-trip from an agent’s
 1472 candidate nest to the original home nest and back, eventually ending
 1473 up with no state changes.
 - 1474 • An ant in the states $follow_T$ or $search_T$ has the same options and vari-
 1475 able changes as in $follow_E$ or $search_E$ respectively, but the resulting

1476 state are sub-scripted with T except the “carry” action.

- 1477 • An ant in $arrive_T$ state has the same options and variable changes as
- 1478 in $arrive_A$, but with “reject” action leading to $transport_T$.

1479 10.2. Simulation Details

1480 10.2.1. Sample Configuration File

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

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

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

1481 10.2.2. Data Structures and Global Variables

1482 We define four native data structures, as shown in Fig. 1. The global
 1483 variables include 1) the transition tables defined in Fig. 3, 2) *Nests*, the
 1484 array of all nests including the home nest which by default has quality
 1485 0 and id 0, and 3) *Ants*, the array of all ants in the colony.

1486 10.2.3. Simulation Overview

1487 We describe our algorithm implementation in details below. Our exe-
 1488 cutable software and instructions are available upon request.

1489 Consider a colony of size num_ants where all the ants start the house-
 1490 hunting task synchronously. We divide the total time to completion
 1491 into *rounds*, with a maximum round number of *total_runs_per_setup*.
 1492 At the beginning of round t , no ant has transitioned yet (instantiate
 1493 $Trans = \emptyset$). Then a random permutation of all *ant_ids* is generated
 1494 as the order of execution. When an ant gets her turn during this
 1495 round, she first checks if her *ant_id* is in *Trans*. If so, she does nothing.
 1496 Otherwise, knowing its id and current state, she chooses an action
 1497 for this round according to the probability distribution defined in the
 1498 **select-action** function.

1499 The action picked by an ant x has an *action_type*, a receiving ant id,
 1500 and a nest id. Please note here that in real ant colonies, an action
 1501 can involve either just a single ant, or a pair of ants (tandem run and
 1502 carry). In the single ant action case, the receiving ant's id is assigned
 1503 value -1 . In the pair ant action case, the action includes the valid
 1504 *ant_id* of the receiving ant y . Similarly, not all actions require a nest,
 1505 in which case the nest id for the action is -1 .

1506 By looking up the *Ants* array, x can also get the current external state
 1507 of all ants including the receiving ant y , if any, of the picked action.
 1508 These values are enough for x to call the **transition** function, and adds
 1509 its own id to *Trans*. The special case handling is detailed in Section
 1510 2.2.3, including the case where y might also call a **transition** function
 1511 and adds itself to *Trans*.

1512 When one round finishes, each ant has had one chance to initiate or
 1513 receive an action, and potentially has a new state. Repeat rounds like

1514 the above until the criteria is met for convergence with persistence, or
1515 until the program reaches the maximum number of rounds specified in
1516 the configuration file.