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An Upper and Lower Bound for the Convergence Time of House-Hunting in *Temnothorax* Ant Colonies

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ABSTRACT

We study the problem of house-hunting in ant colonies, where ants reach consensus on a new nest and relocate their colony to that nest, from a distributed computing perspective. We propose a house-hunting algorithm that is biologically inspired by *Temnothorax* ants. Each ant is modeled as a probabilistic agent with limited power, and there is no central control governing the ants. We show an $\Omega(\log n)$ lower bound on the running time of our proposed house-hunting algorithm, where n is the number of ants. Furthermore, we show a matching upper bound of expected $O(\log n)$ rounds for environments with only one candidate nest for the ants to move to. Our work provides insights into the house-hunting process, giving a perspective on how environmental factors such as nest quality or a quorum rule can affect the emigration process.

Keywords: ant colony, collective behavior, convergence time, decision-making.

1. INTRODUCTION

Recently, there has been an interest in the distributed computing community ontudying biologically inspired algorithms. Tissues found within the human body and insect colonies of ants and bees are good examples of naturally occurring systems where there are many agents with limited power, a global goal, and no central control. Interestingly, an ant colony as a whole exhibits a high level of collective intelligence and is able to achieve global goals, such as foraging for food (Feinerman and Korman, 2012; Feinerman et al., 2012; Emek et al., 2014; Lenzen et al., 2014) and relocating to new nests (Ghaffari et al., 2015; Zhao et al., 2021). It is puzzling how the distributed system is able to quickly reach consensus through local communications, especially given the high noise levels observed in nature.

The house-hunting process in *Temnothorax* ant colonies is a naturally occurring algorithmic task that is closely related to consensus, a fundamental problem in distributed computing theory. The goal of the ants

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is to relocate the colony of ants to a new nest with superior quality. During the house-hunting process, a colony is able to reach consensus on a new nest and execute the move of the entire colony, even though each individual actively scouting ant has information about only a small subset of the new candidate nests.

In 2015, Ghaffari et al. (2015) modeled the ant colony house-hunting process as a distributed algorithm on independent random agents. They also showed theoretical guarantees on the number of rounds required for various house-hunting algorithms under their model to converge. Recently, Zhao et al. (2021) developed a simulator that closely mimics the ants' behaviors on both individual and colony levels. The simulator is based on the agent-based model of ant colony house-hunting process that Pratt et al. (2005) created by studying the videotaped behavior of ants.

Zhao et al. showed that their simulator is biologically plausible in that it accurately reflects many behaviors observed in real ant colonies, and their simulator is also useful for predicting some of the behaviors of ants that are harder for biologists to directly study in experiments. However, there are no theoretical bounds on the convergence speed of the algorithm presented by Zhao et al.

We present a mathematical agent-based model algorithm for the house-hunting emigration process that takes into account the different ways that ants behave and interact with each other depending on the phases and states that they are in. The network of states in our model captures the important dynamics of the models used by biologists, Pratt et al. (2005) and Zhao et al. (2021). As a result, our algorithm is biologically plausible while still tractable to rigorous analysis. We show that the theoretical guarantees on the running time of our algorithm are similar to those of the algorithms considered by Ghaffari et al.

Our work has many implications for both the biology community and the computer science community. Natural algorithms have evolved over time to have many advantageous properties. For example, algorithmic tasks carried out by collections of living beings are usually highly adaptive to different types of environments, robust to noise, and also optimized in terms of their speed and accuracy. Thus, insights from these biological algorithms can inspire more robust efficient algorithms for distributed computer systems, such as robot swarms (Krieger et al., 2000).

Our work develops a biologically inspired algorithm for house-hunting that can be easily implemented and is also tractable to rigorous analysis. In addition, using mathematical tools to analyze the house-hunting algorithm can allow for a better understanding of the properties of ant colonies that are harder for biologists to directly observe. Our work provides insight into how efficient consensus in ant colony house-hunting is affected by nest qualities, the quorum threshold, and other environmental parameters.

1.1. The house-hunting process

Temnothorax ants often search for and move to new nests, as living in favorable nests is important to the survival of their colony. Their moving process is highly distributed: each individual ant has limited information and communication, and there is no central control governing the emigration process.

Ant colonies are typically composed of active and passive ants (Pratt et al., 2005). Active ants execute the emigration, while passive ants, such as brood items or inactive adult ants, are transported to new nests by active ants.

Biologists have observed that the house-hunting process involves several stages. Active ants search for nests, assess nests, recruit other ants, and transport other ants. Once an active ant has found a new nest of satisfactory quality, it moves on to the recruitment phase, where it recruits other active ants to the new nest via *tandem runs* (Möglich, 1978; Richardson et al., 2007). Should the population of active ants in a new nest surpass a *quorum threshold*, then active ants in that nest can commit to that nest and begin *transporting* (i.e., picking up and carrying) other ants from the old nest to the new nest (Pratt et al., 2002). These transports speed up emigration to the new nest.

Scientists believe that ants are able to assess the population density at a nest using their encounter rates with other ants at the site (Pratt, 2005). We assume that ants consider nests of roughly equal sizes so that by measuring the encounter rate, the ants can make decisions based on the population at a nest. We assume that ants are similarly able to determine active and passive ant populations at a nest using the method of encounter rates.

1.2. Main results and organization

In Section 2, we present a biologically plausible house-hunting algorithm that is tractable to analysis. We incorporated biological insights from Pratt et al. (2005) and Zhao et al. (2021) into our house-hunting algorithm.

Ghaffari et al. (2015) showed a lower bound of $\Omega(\log n)$ on the number of rounds required for any house-hunting algorithm under their model of house-hunting to converge with high probability. While there is a subtle difference between our model and the model considered by Ghaffari et al. that affects the lower bound proof, we show in Section 3 that the lower bound of $\Omega(\log n)$ holds for our model as well.

In Section 4, we consider the special case where there are two nests in the environment. We show that our house-hunting algorithm takes expected $O(\log n)$ rounds to converge, assuming that the quorum threshold falls within a certain range. By our lower bound result, this upper bound is tied up to a constant factor. It would be interesting to extend this expected upper bound result to environments with more nests in future work.

Finally, in Section 5, we discuss possible modifications to our house-hunting algorithm and directions for future research.

2. MODEL

We present a model of *Temnothorax* ants' house-hunting process that is both tractable to analysis and biologically plausible. This algorithm is primarily inspired by the agent-based model for house-hunting in ant colonies introduced in Zhao et al. (2021), which produces simulated behaviors of ants that are consistent with empirical observations, but has no proven theoretical guarantees. Like the model in Zhao et al. (2021), our algorithm has many parameters that can be tuned to reflect changing environmental conditions and varied behaviors of ants observed in nature.

Our model differs in that we reduce the number of internal variables stored for each ant and the number of possible states that the ants can be in, thus simplifying the rules for how ants change locations and interact with each other. These simplifications make the model tractable for proofs of theoretical guarantees without significantly changing the overall behavior of the system.

In our algorithm, active and passive ants in the colony play different roles in the emigration process. Active ants transition through many states, including searching for a new nest, evaluating a nest, and recruiting other ants to the nest by tandem or transport runs. Passive ants, on the contrary, change location only when transported by an active ant. The biological insights for these design decisions come from Pratt et al. (2005).

2.1. Framework

The environment consists of at least two nests, one of which is the original home nest (OHN) of the colony, or Nest 0. Each nest has an associated *quality*, which is a non-negative real number. The ants are modeled as identical finite state machines that execute computations synchronously in discrete rounds. In each round, an active ant performs at most one call to each of the functions **select_action**, **select_ant**, and **transition**, which are defined in Section 2.2.

Throughout the article, we let n denote the total number of ants, and we let n_a and n_p denote the number of active ants and passive ants, respectively, with $n_a = \Theta(n)$, $n_p = \Theta(n)$, and $n_a + n_p = n$. The location of an ant a is denoted *a.location*, which is one of the nests in the environment. Every active ant a has an associated state, denoted *a.state*, which is one of nine possible states: At Nest$_i$, Search$_i$, Quorum Sensing, Lead Forward, and Transport, for $i \in \{E, C, T\}$. The subscripts $E, C,$ and T stand for Exploration, Canvassing, and Transport, three different phases of active ants described in Zhao et al. (2021). For every ant a, the value of *a.state* begins as At Nest$_\mathrm{E}$ and the value of *a.location* begins as Nest 0. These values are updated by calls to the helper function **transition**.

On every round, active ants can probabilistically select one of two possible actions to take: *advance* or *hold* (Fig. 1). The action that an ant takes determines how its state and location change that round. There are two instances where an action involves two ants. We say that an ant is *committed* to the nest that it is in if it is in the At Nest$_\mathrm{T}$, Search$_\mathrm{T}$, or Transport state. An ant that is committed to the nest that it is in can *transport* another ant to that nest by advancing from the Transport state. Similarly, an active ant can recruit another active ant to the nest that it is in via a *tandem run* by advancing from the Lead Forward state. Transports and tandem runs fail to move a second ant if that second ant has already transitioned on that round.

Like the model from Zhao et al. (2021), our model is parameterized by many adjustable constants. The parameters μ_q and μ_p are the *quality coefficient* and *population coefficient*, respectively. They represent the relative weight that ants give to the quality and population of a nest when evaluating that nest. We denote by lowercase θ the *quorum threshold*, or the fraction of all active ants that must be in a nest before an active

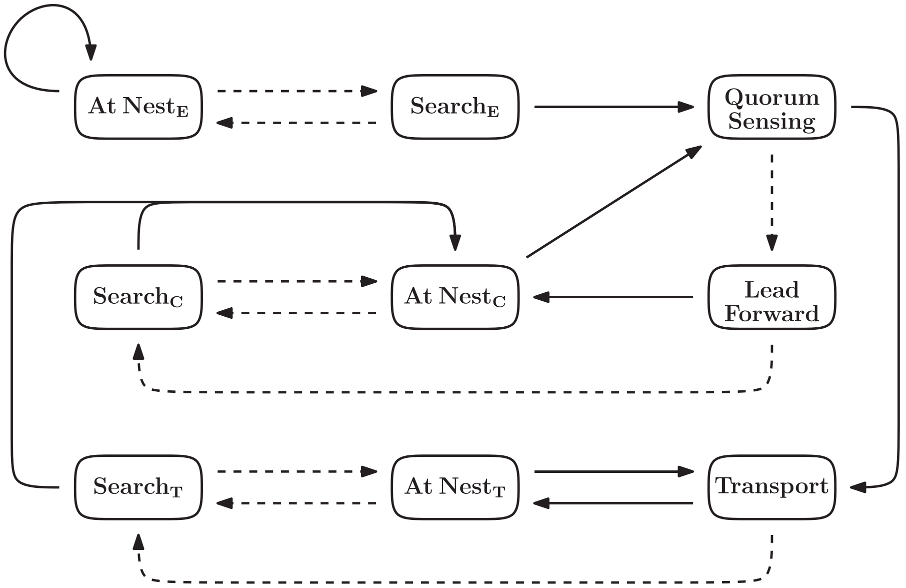

FIG. 1. The state transition diagram. The solid arrows show the state transition that happens when the ant chooses to *advance*; the dashed arrows show the state transition that happens when the ant chooses to *hold*. The transition probabilities are given in (1).

ant can commit to that nest and begin transporting ants to that nest. If the fraction of active ants in Nest 0 ever drops below the quorum threshold, we say that that nest *drops out of competition*, and no active ant can commit to that nest after that point.

The constants c_s, c_f, c_ℓ, and c_t denote the *search constant*, the *follow constant*, the *lead forward constant*, and the *transport constant*. These constants parameterize the probability that the corresponding type of action succeeds. Finally, λ controls for how noisy individual ants' decision-making is, with higher λ values corresponding to lower individual noise levels. For example, when an ant is searching for nests, a higher λ means that she has a higher probability of moving to a more desirable nest and a lower probability of moving to a less desirable nest, where the desirability of a nest depends on both the quality and population of that nest.

All constants other than λ range between 0 and 1; λ ranges from 1 to 16 (Zhao et al., 2021). See Table 1 for an example of values used for these parameters in experiments performed in Zhao et al. (2021).

2.2. Helper functions

This subsection defines the helper functions that are called in the house-hunting algorithm, which is given in Section 2.3.

select_action(a): The input is an ant a. Let n' be a nest chosen uniformly at random from all of the nests other than $a.location$. Let q be the quality of $a.location$, and let p and p_a be the number of ants and active ants in that nest, respectively. Finally, let q' and p' denote the quality and population of nest n'. The ant probabilistically chooses an action u, sampled from a Bernoulli random variable $\mathbf{u} \in \{\text{advance},\ \text{hold}\}$ with parameters that depend on $a.state$ as shown in Eq. (1). The function **select_action(a)** returns (u, n').

TABLE 1. AN EXAMPLE OF A SET OF PARAMETER VALUES THAT ARE BIOLOGICALLY PLAUSIBLE

Parameter	*Value*	*Source*
Quality coefficient μ_q	0.25	Trial-and-error from Zhao et al. (2021)
Population coefficient μ_p	0.35	Trial-and-error from Zhao et al. (2021)
Quorum threshold θ	0.15	Pratt et al. (2002), Franks et al. (2015)
Search constant c_s	0.025	Trial-and-error from Zhao et al. (2021)
Follow constant c_f	0.4	Pratt (2008), Glaser and Grüter (2018)
Lead forward constant c_ℓ	0.6	Trial-and-error from Zhao et al. (2021)
Transport constant c_t	0.7	Pratt et al. (2005)
λ	8	Trial-and-error from Zhao et al. (2021)

$$\Pr[\mathbf{u} = \text{advance} | a.\mathit{state} = \text{At Nest}_i] = \left(1 + e^{-\lambda\left(\mu_q \cdot q + \mu_p \cdot \frac{p}{n}\right)}\right)^{-1} \text{for } i \in \{\text{E, C, T}\} \tag{1}$$

$$\Pr[\mathbf{u} = \text{advance} | \, a.\mathit{state} = \text{Search}_i] = c_s \cdot \left(1 + e^{-\lambda\left(\mu_q \cdot (q' - q) + \mu_p \cdot \frac{p' - p}{n}\right)}\right)^{-1} \text{ for } i \in \{\text{E, C, T}\}$$

$$\Pr[\mathbf{u} = \text{advance} | \, a.\mathit{state} = \text{Quorum Sensing}] = \begin{cases} 1 & \text{if quorum has been met — that is, } p_a > \theta \cdot n_a \\ & \text{and } a.\mathit{location} \text{ has not dropped out of competition} \\ 0 & \text{otherwise} \end{cases}$$

$$\Pr[\mathbf{u} = \text{advance} | \, a.\mathit{state} = \text{Transport}] = c_t$$

$$\Pr[\mathbf{u} = \text{advance} | \, a.\mathit{state} = \text{Lead Forward}] = \begin{cases} c_\ell & \text{if } q > q' \\ 0 & \text{otherwise} \end{cases}$$

select_ant(a, n′, action): This function takes as input an ant a, a nest n', and an action *action*. If *action* is hold, then this function immediately returns *null*. First, we set a' to null. If $a.\mathit{state}$ is Lead Forward and there is at least one active ant in nest n', then let a' be an active ant chosen uniformly at random from n'. If $a.\mathit{state}$ is Transport and there is at least one passive ant in nest n', then let a' be a passive ant chosen uniformly at random from n'. We return a' with probability c_f and return *null* otherwise. Note that the returned ant cannot be a because a is not in nest n'.

transition(a, a′, n′, action): This function takes as input ants a and a', a nest n', and an action *action*.

If $a.\mathit{state}$ is Search_i for any $i \in \{E, C, T\}$ and *action* is advance, then we set $a.\mathit{location}$ to n'. If $a.\mathit{state}$ is Lead Forward or Transport and *action* is advance, then we set $a'.\mathit{location}$ to $a.\mathit{location}$. We set $a.\mathit{state}$ to the state obtained by starting from $a.\mathit{state}$ and following the arrow corresponding to *action* in the state transition diagram (Fig. 1). If a' is not null, we set $a'.\mathit{state}$ to At Nest_E.

2.3. Algorithm

With the helper functions defined, we are ready to present the house-hunting algorithm. Let P be a permutation of the integers 1 to n_a chosen uniformly at random for every round, and the active ants are denoted a_i for $i \in \{1, \ldots, n_a\}$.

Algorithm 1: One Round of the HOUSE-HUNTING Algorithm

```
$M$: a set of ants, initially $\emptyset$
for $i = 1$ to $n_a$ do
    if $a_{P(i)} \notin M$ then
        $action, n' :=$ select_action($a_{P(i)}$)
        $a' :=$ select_ant($a_{P(i)}, n', action$)
        if $a' \in M$ then
            $a' \leftarrow null$
        end
        transition($a_{P(i)}, a', n', action$)
        $M := M \cup \{a_{P(i)}\} \cup \{a'\}$
    end
end
```

Algorithm 1 shows one round of the house-hunting algorithm. We study how many times the procedure given in Algorithm 1 repeats until all of the passive ants have moved from Nest 0 to a *winning nest*, a nest that has better quality than Nest 0. When this happens, we say that the algorithm *converges*. We note that not all of the active ants are required to be in the winning nest (WN) when the algorithm converges since the active ant population is more mobile.

In Algorithm 1, the set M serves to make sure that each ant transitions at most once: either actively by initiating an action or passively by getting recruited. If there are conflicts between actions involving two ants (i.e., tandem runs or transports), then P serves as a tie breaker between the conflicting actions.

In short, for every $i \in \{1, \ldots, n_a\}$, if ant a_i has not been recruited (by a tandem run or transport) by the time all active ants preceding a_i in the permutation have transitioned in a given round, the ant a_i will probabilistically select an action to take using the **select_action** function and select an accompanying ant a' using the **select_ant** function. If a_i is not successfully transporting or leading forward, then a' will be set to *null*. Finally, the **transition** helper function updates the states and locations of ants a_i and a' to reflect the changes caused by the action that ant a_i executed.

3. A LOWER BOUND

In this section, we asymptotically lower bound the number of rounds required for a colony of ants to complete the house-hunting process with high probability. We use ideas from the lower bounds on spreading a rumor in a graph from Karp et al. (2000) and proof methods from Ghaffari et al. (2015). We also use terminology from Ghaffari et al. (2015): an *informed* ant knows the location of the WN, and an *ignorant* ant does not know.

Ghaffari et al. (2015) proved an asymptotic lower bound on the convergence rate of their algorithm that grew logarithmically in the number of ants. There is a subtle difference between our model and that of Ghaffari et al.'s that affects the proof of the lower bound. In the model used by Ghaffari et al., the probability that any ignorant ant becomes informed on any given round can be upper bounded by a constant less than 1 (Lemma 3.1 of (Ghaffari et al., 2015).

In contrast, in our algorithm, the probability that a given passive ant in the OHN gets transported to the WN on any given round cannot be upper bounded by a constant less than 1: when there are many active ants in the WN trying to transport ants from the OHN to WN and a few passive ants in the OHN, each passive ant in the OHN gets transported with high probability.

Even though we are not able to lower bound the probability that any ignorant ant remains ignorant in any given round of our algorithm, we are able to lower bound this quantity for a fraction of the passive ants, as shown in the following lemma.

Lemma 1. *Let* $m = \frac{n_a}{n_p}$. *If* $n_p \geq 4$, *then for any given round r where there are at least* $\frac{n_p}{2}$ *ignorant passive ants in Nest 0 at the beginning of round r, a passive ant in Nest 0 that is ignorant at the beginning of round r remains ignorant at the end of round r with probability at least* $\left(\frac{1}{16}\right)^m$.

Proof. Let $B \geq \frac{n_p}{2} \geq 2$ be the number of ignorant passive ants in Nest 0 at the beginning of round r. The only way for an ignorant passive ant to become informed is for that ant to be transported by an active ant. There are at most n_a active ants transporting passive ants out of Nest 0 on any given round. While there are passive ants in Nest 0, an active ant transporting from that nest chooses one of those passive ants to transport uniformly at random. Thus, the probability that any given passive ant does not get transported during round r is at least

$$\left(\frac{B-1}{B}\right)^{n_a}.$$

Using the fact that $\left(\frac{x-1}{x}\right)^x \geq \frac{1}{4}$ when $x \geq 2$, we have

$$\left(\frac{B-1}{B}\right)^{n_a} \geq \left(\frac{1}{4}\right)^{\frac{n_a}{B}} \geq \left(\frac{1}{4}\right)^{\frac{2n_a}{n_p}},$$

finishing the proof of the lemma. □

Ghaffari et al. (2015) proved a lower bound of $\Omega(\log n)$ on the running time of their house-hunting algorithm. Their proof depended on a lemma that stated that all ignorant ants stay ignorant with constant probability during each round; we showed in Lemma 1 that this result is true for $\frac{n_p}{2}$ of the passive ants. This discrepancy by a constant factor does not affect the asymptotic behavior of the algorithm. More formally, we use Lemma 1 and proof methods from Ghaffari et al. (2015) to show the following theorem:

Theorem 1. *If* $n_p \geq 4$, *then for any constant* $c > 0$, *our proposed house-hunting algorithm requires* $\Omega(\log n)$ *rounds for all of the passive ants to move from Nest 0 to the WN with probability at least* $\frac{1}{n^c}$.

Proof. Let $m = \frac{n_a}{n_p}$, and let $\rho = \left(\frac{1}{16}\right)^m$. Because $n_a = \Theta(n)$ and $n_p = \Theta(n)$, we have $\rho = \Theta(1)$. Let S be the set of the first $\frac{n_p}{2}$ passive ants to become informed. We investigate the number of rounds required for all of the ants in S to become informed with high probability. By Lemma 1, with probability at least ρ, an ant in S that is ignorant at the beginning of round r remains ignorant at the end of round r.

For every ant $a \in S$ and every round r, let Y_r^a be a Bernoulli random variable with $\Pr[Y_a^r = 1] = \rho^r$. Let $Y_r = \sum_{a \in S} Y_r^a$. We define random variable S_r to be the number of ants in S ignorant after r rounds. Note that for every $a \in S$ and every round r, $\Pr[Y_a^r = 1] = \rho^r$ lower bounds the probability that ant a is ignorant after r rounds. Thus, we have

$$\Pr[S_r < x] \le \Pr[Y_r < x] \text{ for any round } r \text{ and any } x. \tag{2}$$

For $r = \frac{1}{2}\log_{\rho^{-1}}\left(\frac{n_p^2}{4n}\right) - \log_{\rho^{-1}}(8c)$, we have $\mathbb{E}[Y_r] = |S|\rho^r = 8c\sqrt{n}$, and

$$\begin{aligned}\Pr\left[S_r < \frac{\mathbb{E}[Y_r]}{2}\right] &\le \Pr\left[Y_r < \frac{\mathbb{E}[Y_r]}{2}\right] \text{(Using (2))}\\ &\le e^{-\frac{\mathbb{E}[Y_r]}{8}} \text{ (Chernoff bound)}\\ &= e^{-c\sqrt{n}}\\ &< \frac{1}{n^c}. \left(e^{-\sqrt{x}} < \frac{1}{x} \text{for } x > 0\right)\end{aligned}$$

Therefore, with probability at least $1 - \frac{1}{n^c}$, at least $4c\sqrt{n}$ passive ants are ignorant after $\frac{1}{2}\log_{\rho^{-1}}\left(\frac{n_p^2}{4n}\right) - \log_{\rho^{-1}}(8c) = \Theta(\log n)$ rounds. Thus, the number of rounds required for all of the passive ants to move to the WN with probability at least $\frac{1}{n^c}$ is $\Omega(\log n)$. □

4. AN EXPECTED UPPER BOUND FOR SINGLE-NEST EMIGRATIONS

In this section, we consider an environment with only two nests: Nest 0 (with quality q_0) and Nest 1 (with quality $q_1 > q_0$). All of the ants are in Nest 0 in the At Nest$_\mathrm{E}$ state at the beginning of Round 1, and we investigate how long it takes for the house-hunting algorithm to converge as the number of ants n varies.[1]

Since an active ant will change location if it advances from a Search state, the frequency at which ants are in Search states is of interest to us.

Definition 1. *For every integer $k > 0$, we define $R_0^{(k)}$ and $R_1^{(k)}$ using the states and locations of the active ants at the beginning of round k. Random variable $R_0^{(k)}$ is 1 if there are no active ants in Nest 0; otherwise, $R_0^{(k)}$ is the fraction of active ants in Nest 0 that are in one of the Search states (Search$_\mathrm{E}$, Search$_\mathrm{C}$, or Search$_\mathrm{T}$). Similarly, random variable $R_1^{(k)}$ is 0 if there are no active ants in Nest 1; otherwise, $R_1^{(k)}$ is the fraction of active ants in Nest 1 that are in one of the Search states. We define $f_0 := \min_{k>1} \mathbb{E}\left[R_0^{(k)}\right]$ and $f_1 := \max_k \mathbb{E}\left[R_1^{(k)}\right]$.*

We do not explicitly compute f_0 and f_1 since this would require intensive computations. Instead, we make the following useful observation:

Observation 1. *We have $f_0, f_1 > \varepsilon$ for some constant $\varepsilon > 0$ that is independent of n.*

Proof. Since all ants start out in the At Nest$_\mathrm{E}$ state in Nest 0, we have $R_0^{(1)} = 0$. For $k > 1$, $\Pr\left[R_0^{(k)} > 0\right] > 0$ since there is the possibility that an active ant in Nest 0 stays in the At Nest$_\mathrm{E}$ state until it moves to the Search$_\mathrm{E}$ state during the $(k-1)^{\text{th}}$ round. Thus, $\mathbb{E}\left[R_0^{(k)}\right] > 0$ for $k > 1$, so $f_0 > 0$.

If $f_1 = 0$, then that means that either no active ants ever enter Nest 1 or the expected fraction of active ants in Nest 1 that are in a Search state is 0 for every round. Both of these statements are clearly not true, and so, we have $f_1 > 0$ by contradiction.

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[1] Our algorithm relaxes some assumptions made in the algorithms by Ghaffari et al. (2015). In their optimal algorithm, nests with a decreasing population drop out of competition, and in their simple algorithm, ants only search for nests at the beginning of the algorithm. Because our algorithm does not use these assumptions, the proof methods that they use to show their upper bound results do not work for our algorithm.

Because the state transition diagram has a recurrent class that is finite, aperiodic, and irreducible, the states in that class are associated with unique steady-state probabilities. The states Search_C and Search_T are recurrent states, and so, their steady-state probabilities are positive. The values $\mathbb{E}\left[R_i^{(k)}\right]$ for $i \in \{0, 1\}$ only depend on the transition probabilities of the model and k, and they converge to the corresponding steady-state probabilities, which also only depend on the transition probabilities. All of the transition probabilities of the model can be upper and lower bounded by positive constants independent of n. Thus, f_0 and f_1 can also be lower bounded by a constant independent of n. □

Recall from Section 2 that we say that the algorithm converges when all of the passive ants are in the WN. In this section, we prove the main theorem (Theorem 2), which says that the algorithm converges in expected $O(\log n)$ rounds in an environment with two nests as long as some restrictions on the parameters are satisfied. We begin with a definition.

Definition 2. *The function* $a : \mathbb{R} \to \mathbb{R}$ *is defined as follows:*

$$a(x) = n_a \left(\frac{\frac{f_0}{f_1} - x}{\frac{f_0}{f_1} + e^{\alpha}} \right),$$

where $\alpha = -\lambda(\mu_q(q_1 - q_0) - \mu_p)$.

Theorem 2. *For any small constant* $\varepsilon \in \left(0, \frac{f_0}{f_1}\right)$, *let random variable* R_ε *denote the number of rounds required for at least* $a(\varepsilon)$ *of the active ants and all of the passive ants to move from Nest 0 to Nest 1. If the quorum threshold satisfies* $1 - \frac{a(\varepsilon)}{n_a} < \theta < \frac{a(\varepsilon)}{n_a}$, *then* $\mathbb{E}[R_\varepsilon] = O(\log n)$.

We note that a condition of Theorem 2 is that the quorum threshold θ must fall within the range $\left(1 - \frac{a(\varepsilon)}{n_a}, \frac{a(\varepsilon)}{n_a}\right)$. In particular, we see in Proposition 2 that the lower bound on the quorum threshold guarantees that backward transports from Nest 1 to Nest 0 cease to happen after $O(\log n)$ rounds. The upper bound on the quorum threshold simply guarantees that the quorum will be met at Nest 1, allowing for transports to that nest. When we plug in the biologically plausible values $\lambda = 8$, $\mu_q = .25$, $\mu_p = .35$, $q_1 = 2$, $q_0 = 0$, let $\varepsilon = .00001$, and use the estimate $\frac{f_0}{f_1} \approx 1$, we find that the condition becomes $\theta \in (.2315, .7685)$. If we instead plug in $q_1 = 3$, then the condition becomes $\theta \in (.0392, .9608)$. By comparing with Section 2.1, we see that the bounds on the quorum threshold required by the theorem are reasonable and not overly restrictive.

We further note that the condition $1 - \frac{a(\varepsilon)}{n_a} < \theta < \frac{a(\varepsilon)}{n_a}$ is sufficient but not proven to be necessary for the algorithm to converge in $O(\log n)$ rounds. In addition, it is possible to choose ε, parameter values, and nest qualities such that $1 - \frac{a(\varepsilon)}{n_a} > \frac{a(\varepsilon)}{n_a}$. In this case, it is impossible for the condition to be satisfied. Intuitively, this means that for such a set of parameter values, the positive difference $q_1 - q_0$ is not large enough; in other words, Nest 1 is not better than Nest 0 by enough for efficient convergence to be guaranteed by the theorem. More formally, using the estimate $\frac{f_0}{f_1} - 2\varepsilon \approx 1$, the condition $1 - \frac{a(\varepsilon)}{n_a} < \frac{a(\varepsilon)}{n_a}$ becomes $q_1 - q_0 > \frac{\mu_p}{\mu_q}$, a lower bound on the difference in quality between the two nests in order for efficient convergence to be guaranteed by Theorem 2. It would be interesting for this prediction about the effect of nest qualities on ant colony house-hunting to be tested in an experiment with real ants.

We prove Theorem 2 by separately examining the emigration of active and passive ants. We examine active ant emigration in Section 4.1, and we examine passive ant emigration in Section 4.2.

4.1. *Active ant emigration*

In this subsection, we focus on the emigration of active ants. We use the quantities f_0 and f_1 from Definition 1 to study the expected number of ants that move between the nests during each round.

Lemma 2. *Suppose there are* x *active ants in Nest 0 at the beginning of a round* $r > 1$. *The expected number of active ants that move from Nest 0 to Nest 1 during round* r *is at least*

$$\frac{c_s \cdot f_0 \cdot x}{1 + e^{-\lambda(\mu_q(q_1 - q_0) - \mu_p)}}.$$

Proof. We can see that active ants change location only when they advance from a Search state or get recruited to a new nest by another active ant via a tandem run. In our model, a tandem run can only cause an active ant to be recruited from an inferior nest to a nest with better quality. Thus, tandem runs will only speed up the rate at which ants move from Nest 0 to Nest 1, and so, we can disregard the population changes caused by tandem runs without loss of generality and focus on ants that change locations by advancing from the Search state.

We denote by p_0 and p_1 the population in Nest 0 and Nest 1 at the beginning of round r, respectively. The probability p that an active ant in a Search state at Nest 0 advances, thus moving to Nest 1, is

$$\begin{aligned} p &= \frac{c_s}{1+e^{-\lambda(\mu_q(q_1-q_0)+\mu_p(p_1-p_0)/n)}} \\ &\geq \min_{(p_0,p_1)\in\{0,1,\dots,n\}^2} \frac{c_s}{1+e^{-\lambda(\mu_q(q_1-q_0)+\mu_p(p_1-p_0)/n)}} \\ &= p' := \frac{c_s}{1+e^{-\lambda(\mu_q(q_1-q_0)-\mu_p)}}, \end{aligned}$$

where the last line follows because p is minimized when $p_1 - p_0$ is minimized, which is achieved when $p_0 = n$ and $p_1 = 0$.

The expected number of active ants in a Search state at Nest 0 at the beginning of round r is at least $f_0 \cdot x$. Thus, the expected number of active ants that move from Nest 0 to Nest 1 during round r is at least $f_0 \cdot x \cdot p'$. ☐

We can obtain the following lemma using the same reasoning that we used in the proof of Lemma 2.

Lemma 3. *Suppose there are x active ants in Nest 0 at the beginning of a round r. The expected number of active ants that move from Nest 1 to Nest 0 during round r is at most*

$$\frac{c_s \cdot f_1 \cdot (n_a - x)}{1+e^{-\lambda(\mu_q(q_0-q_1)+\mu_p)}}.$$

Proof. As in the proof of Lemma 2, we only focus on ants that move nests by advancing from a Search state.

We denote by p_0 and p_1 the population in Nest 0 and Nest 1 at the beginning of round r, respectively. We upper bound the probability q that an active ant in a Search state at Nest 1 advances, thus moving to Nest 0:

$$\begin{aligned} q &= \frac{c_s}{1+e^{-\lambda(\mu_q(q_0-q_1)+\mu_p(p_0-p_1)/n)}} \\ &\leq \max_{p_0,p_1\in\{0,1,\dots,n\}^2} \frac{c_s}{1+e^{-\lambda(\mu_q(q_0-q_1)+\mu_p(p_0-p_1)/n)}} \\ &= q' := \frac{c_s}{1+e^{-\lambda(\mu_q(q_0-q_1)+\mu_p)}}, \end{aligned}$$

where the last line follows because q is maximized when $p_0 - p_1$ is maximized, which is achieved when $p_0 = n$ and $p_1 = 0$.

The expected number of active ants in a Search state at Nest 1 at the beginning of round r is at most $f_1 \cdot (n_a - x)$. Thus, the expected number of active ants that move from Nest 1 to Nest 0 during round r is at most $f_1 \cdot (n_a - x) \cdot q'$. ☐

Now, we put Lemma 2 and Lemma 3 together to show that the number of rounds required for a constant fraction of the active ant population to move to Nest 1 is independent of the size of the ant colony. Recall the definitions of function $a(\cdot)$ and constant α from Definition 2.

Lemma 4. *Let random variable A_r denote the number of active ants in Nest 1 after r rounds. For every constant $\delta \in \left(0, \frac{f_0}{f_1}\right)$, there exists a constant c, independent of n, such that $\mathbb{E}[A_c] \geq a(\delta)$.*

Proof. Let random variable Y_x denote the number of ants that Nest 1 gains during a round $r > 1$ that begins with x active ants in Nest 0. Putting Lemma 2 and Lemma 3 together, we have

$$\begin{aligned} \mathbb{E}[Y_x] &\geq \frac{c_s \cdot f_0 \cdot x}{1+e^{\alpha}} - \frac{c_s \cdot f_1 \cdot (n_a - x)}{1+e^{-\alpha}} \\ &= \Theta\left(\frac{f_0}{f_1} x(1+e^{-\alpha}) - (n_a - x)(1+e^{\alpha})\right) \\ &= \Theta\left(x\left(\frac{f_0}{f_1}\cdot e^{-\alpha}+1\right)(1+e^{\alpha}) - n_a(1+e^{\alpha})\right) \\ &= \Theta\left(x\left(\frac{f_0}{f_1}\cdot e^{-\alpha}+1\right) - n_a\right). \end{aligned}$$

If $x \geq n_a - a(\delta) = n_a\left(\frac{e^{\alpha}+\delta}{\frac{f_0}{f_1}+e^{\alpha}}\right)$, we have

$$\begin{aligned}\mathbb{E}[Y_x] &= \Omega\left(n_a\left(\frac{e^{\alpha}+\delta}{\frac{f_0}{f_1}+e^{\alpha}}\right)\left(\frac{f_0}{f_1}\cdot e^{-\alpha}+1\right)-n_a\right)\\ &= \Omega\left(n_a\left(\frac{\delta}{e^{\alpha}}\right)\right)\\ &= \Omega(n).\end{aligned}$$

Thus, while there are at least $n_a - a(\delta)$ active ants in Nest 0, Nest 0 loses $\Omega(n)$ active ants and Nest 1 gains $\Omega(n)$ active ants in expectation during every round. As a result, the expected number of ants in Nest 0 drops down to at most $n_a - a(\delta)$ in a constant number of rounds. □

Now that we have shown that the number of rounds required for expected $a(\varepsilon)$ active ants to move to Nest 1 is independent of the size of the ant colony, we use that result to show that the expected number of *rounds* required for $a(\varepsilon)$ active ants to move to Nest 1 is also independent of colony size. In particular, now our random variable is the number of rounds, rather than the number of active ants in Nest 1.

Proposition 1. *For any constant* $\varepsilon \in \left(0, \frac{f_0}{f_1}\right)$, *let random variable* R_ε *denote the number of rounds before Nest 1 first has at least* $a(\varepsilon)$ *active ants. We have that* $\mathbb{E}[R_\varepsilon] = O(1)$.

Proof. We choose constant δ such that $0 < \delta < \varepsilon < \frac{f_0}{f_1}$. Let c be the number of rounds required for an expected $a(\delta)$ of the active ants to move to Nest 1. By Lemma 4, c is a constant independent of n.

We denote by the random variable A the number of active ants that Nest 1 gains in c rounds. By definition, $\mathbb{E}[A] = a(\delta) > a(\varepsilon)$. Using the fact that $A \leq n$, we upper bound $\Pr[A \leq a(\varepsilon)]$:

$$\mathbb{E}[A] \leq \Pr[A \leq a(\varepsilon)]a(\varepsilon) + (1 - \Pr[A \leq a(\varepsilon)])n$$

$$\Rightarrow \Pr[A \leq a(\varepsilon)] \leq \frac{n - a(\delta)}{n - a(\varepsilon)}.$$

For any integer $r \geq 1$, we have that $\Pr[R_\varepsilon = r]$ is upper bounded by

$$\Pr[R_\varepsilon \geq r] \leq \Pr[A \leq a(\varepsilon)]^{\lfloor \frac{r}{c} \rfloor} \leq \left(\frac{n - a(\delta)}{n - a(\varepsilon)}\right)^{\lfloor \frac{r}{c} \rfloor}$$

because in order for $R_\varepsilon \geq r$, Nest 1 must have gained less than $a(\varepsilon)$ ants every consecutive c rounds since the start of the algorithm.

We thus have

$$\begin{aligned}\mathbb{E}[R_\varepsilon] &= \sum_{r=1}^{\infty} \Pr[R_\varepsilon = r] \cdot r\\ &\leq \sum_{r=1}^{\infty} \left(\frac{n - a(\delta)}{n - a(\varepsilon)}\right)^{\lfloor \frac{r}{c} \rfloor} \cdot r\\ &= \Theta(1).\end{aligned}$$

The last equality follows because $\frac{n-a(\delta)}{n-a(\varepsilon)}$ is less than 1 and has no dependency on n since $a(\delta), a(\varepsilon) = \Theta(n_a) = \Theta(n)$, and so, the factors of n in the numerator and denominator cancel out. □

4.2. Passive ant emigration

Passive ants only change location when they are transported by active ants. Thus, we first examine the changes in the number of transports as the algorithm proceeds. We start by proving a lemma that will be useful for converting bounds on expected number of ants to bounds on expected number of rounds.

Lemma 5. *Consider an environment with n ants. On every discrete round, each ant may independently and probabilistically decide to leave and never come back. Let random variable R denote the number of rounds that it takes for all of the ants to leave. If the expected number of ants that leave on every round is at least* $c \times$ [*the number of ants remaining at the beginning of that round*] *for some constant* $c \in (0, 1]$ *independent of n, then* $\mathbb{E}[R] = O(\log n)$.

Proof. Let $r^* = \log_{1-c}\frac{1}{2n}$, and let random variable A denote the number of ants remaining after r^* rounds. By Markov's Inequality,

$$\Pr[A \geq 1] \leq \mathbb{E}[A] \leq n(1-c)^{r^*} = \frac{1}{2}.$$

Let random variable R_1 denote the number of rounds that it takes for all but at most one ant to leave. For any integer $t \geq 0$, we have that

$$\begin{aligned}\Pr[t \cdot r^* < R_1 \leq (t+1) \cdot r^*] &\leq \Pr[R_1 > t \cdot r^*]\\ &\leq \Pr[A \geq 1]^t\\ &\leq \left(\frac{1}{2}\right)^t.\end{aligned}$$

We use this inequality to bound $\mathbb{E}[R_1]$.

$$\begin{aligned}\mathbb{E}[R_1] &= \sum_{r=1}^{\infty} \Pr[R_1 = r] \cdot r\\ &\leq \sum_{t=0}^{\infty} \Pr[t \cdot r^* < R_1 \leq (t+1)r^*] \cdot (t+1)r^*\\ &\leq r^* \sum_{t=0}^{\infty} \left(\frac{1}{2}\right)^t \cdot (t+1)\\ &= \Theta(\log n).\end{aligned}$$

Now, we investigate $R - R_1$, that is, the number of additional rounds it takes for all of the ants to leave after all but at most one ant already left.

$$\begin{aligned}\mathbb{E}[R - R_1] &\leq \sum_{r=1}^{\infty} \Pr[R - R_1 \geq r] \cdot r\\ &\leq \sum_{r=1}^{\infty} (1-c)^{r-1} \cdot r\\ &= \Theta(1).\end{aligned}$$

Thus, $\mathbb{E}[R] = \mathbb{E}[R_1] + \mathbb{E}[R - R_1] = O(\log n) + O(1) = O(\log n)$. □

Proposition 2. *Let random variable R denote the number of rounds that the algorithm runs for before no more ants perform transports from Nest 1 to Nest 0 for the rest of the algorithm. If the quorum threshold satisfies* $\theta > 1 - \frac{a(\varepsilon)}{n_a}$, *then* $\mathbb{E}[R] = O(\log n)$.

Proof. By Proposition 1, after an expected constant number of rounds, there will be at most $n_a - a(\varepsilon)$ active ants in Nest 0, which is below the quorum threshold. After the fraction of active ants that are in Nest 0 drops below the quorum threshold θ, Nest 0 drops out of competition, and no more active ants will commit to Nest 0 (i.e., advance from the Quorum Sensing state while in Nest 0). After this point, the number of ants committed to Nest 0 cannot increase.

By the reasoning from Lemma 2, a constant fraction of the ants committed to Nest 0 are expected to move to Nest 1 (thus becoming no longer committed to Nest 0) on any given round. Hence, the expected number of ants committed to Nest 0 decreases by a constant factor on each round after the number of active ants in Nest 0 drops below quorum. After Nest 0 drops out of competition, we say that an ant that is not committed to Nest 0 is an ant that has ''left'' in Lemma 5, and we can use Lemma 5 to conclude that there will be no more ants committed to Nest 0 after expected $O(\log n)$ rounds. □

By Proposition 2, we have that the effect of transports from Nest 1 to Nest 0 is negligible after expected $O(\log n)$ rounds. We can now bound the expected number of rounds required for all of the passive ants to be moved to Nest 1.

Proposition 3. *Let random variable R denote the number of rounds required for all of the passive ants to be transported to Nest 1. If the quorum threshold satisfies* $1 - \frac{a(\varepsilon)}{n_a} < \theta < \frac{a(\varepsilon)}{n_a}$, *we have* $\mathbb{E}[R] = O(\log n)$.

Proof. We consider any given round of the algorithm; we let a_1 denote the number of active ants transporting from Nest 0 to Nest 1 at the beginning of that round, and we let p_0 denote the number of passive ants in Nest 0 at the beginning of that round. We break into two cases depending on how a_1 and p_0 compare with each other.

Case 1: $a_1 \leq \frac{1}{2}p_0$.

Each active ant in Nest 1 that is transporting (i.e., advancing from the Transport state) has at least a 50% chance of successfully moving a passive ant to Nest 1 on this round. This is because less than half of the passive ants in Nest 0 could have already been transported by a different active ant during that round. Thus, in this case, the expected number of passive ants that get transported to Nest 1 in this round is at least $\frac{1}{2}\mathbb{E}[a_1]$. If quorum has been met in Nest 1, we expect a constant fraction of the active ants in Nest 1 to be transporting and thus $\frac{1}{2}\mathbb{E}[a_1] = \Theta(n_a) = \Theta(n) = \Omega(p_0)$.

Case 2: $a_1 > \frac{1}{2}p_0$.

The probability that a given passive ant does not get transported is at most

$$\begin{aligned}\left(\frac{p_0 - 1}{p_0}\right)^{a_1} &< \left(\frac{p_0 - 1}{p_0}\right)^{\frac{1}{2}p_0} \\ &\leq \left(e^{-\frac{1}{p_0}}\right)^{\frac{1}{2}p_0} \\ &= e^{-\frac{1}{2}}.\end{aligned}$$

Since every passive ant in Nest 0 has at least a constant probability of getting transported to Nest 1 in this case, the expected number of ants that get transported to Nest 1 in this round is $\Omega(p_0)$.

By Proposition 1, at least $a(\varepsilon) > \theta \cdot n_a$ active ants will be in Nest 1 after an expected constant number of rounds, and by Proposition 2, there will be no more ants performing backward transports from Nest 1 to Nest 0 after an expected $O(\log n)$ rounds. After that, the expected number of passive ants that are transported from Nest 0 to Nest 1 during each round will be $\Omega(p_0)$ in both Case 1 and Case 2. After backward transports cease to happen, we say that a passive ant in Nest 1 is an ant that has "left" in Lemma 1, and we can use Lemma 5 to conclude that all passive ants will be in Nest 1 after expected $O(\log n)$ rounds. □

Finally, putting Proposition 1 and Proposition 3 passive ants together proves Theorem 2.

5. DISCUSSION AND FUTURE WORK

In our work, we presented and analyzed the running time of a biologically plausible house-hunting algorithm. We proved a high probability lower bound of $\Omega(\log n)$ rounds in Theorem 1, which directly implies an expected lower bound of $\Omega(\log n)$ rounds. We also proved an expected upper bound of $O(\log n)$ rounds in Theorem 2 for single-nest emigrations, given that the quorum threshold falls within a certain range.

In particular, without the lower bound on the quorum threshold, we would not be able to show Proposition 2, and the emigration progress may be delayed due to backward transports from the superior nest to the inferior nest. There is a lot of work in the biology community studying the role that the quorum threshold plays in the house-hunting process; as we see with our result, mathematical analyses such as ours can provide possible explanations for why ant colonies have evolved to use quorum sensing to coordinate behaviors and how ants choose a quorum threshold.

The rest of this section discusses future work. It would be interesting to extend Theorem 2 to the general multinest setting to understand how competing nests in the environment affect expected running time; it would also be interesting to derive a corresponding high-probability upper bound on running time. The condition required by Theorem 2 can be approximated as $q_1 - q_0 > \frac{\mu_p}{\mu_q}$, a lower bound on the difference in quality between the two nests in order for efficient convergence to be guaranteed. It would be interesting for this prediction about the effect of nest qualities on ant colony house-hunting to be tested in an experiment with real ants. Furthermore, all of our results are asymptotic; computer simulations or biological experiments can give us more information about the hidden constants in the asymptotic notations.

For the sake of simplicity and for our analysis, we made many simplifications to the model from Zhao et al. (2021), on which our algorithm is based. Although our model consists of fewer states in the state transition diagram than the model in Zhao et al. (2021), our analysis is robust to changes to the state transition diagram, as long as all of the transition probabilities can be bounded by constants independent of the number of ants and the ways that ants change location are unaffected.

The other key difference is that in the model from Zhao et al. (2021), each ant has more internal variables (in addition to the state and location of the ant, which our model uses). For example, the home nest, candidate nest, and previous candidate nest are also stored for each ant. Because of this, the rules for location changes in the model in Zhao et al. (2021) are also more fine-grained, making analysis more complicated. It would be interesting to analyze a house-hunting algorithm that is more similar to the one given in Zhao et al. (2021) as the algorithm in Zhao et al. (2021) has been shown to be biologically plausible by comparison with biological data (Pratt et al., 2005).

In our model, recruitments via tandem runs can only happen from inferior nests to superior nests, and the OHN drops out of competition once the fraction of active ants in that nest drops below the quorum threshold. One potential direction for future research is to analyze our house-hunting algorithm with the modifications that the direction of tandem runs is unrestricted and the OHN never drops out of competition. These two modifications would make the algorithm more general.

See Ghaffari et al. (2015) for other possible extensions to the algorithm that may be included, potentially at the expense of the runtime or simplicity of the algorithm. Some potential extensions include making the algorithm more fault tolerant and relaxing the synchronous round assumption.

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