

Invited Paper: Lack of Quorum Sensing Leads to Failure of Consensus in *Temnothorax* Ant Emigration

Jiajia Zhao^{1*}[0000–0003–3046–5362], Lili Su²[0000–0003–3538–5679], and
Nancy Lynch¹[0000–0003–3045–265X]

¹ Massachusetts Institute of Technology, Cambridge, MA 02139, USA
{jiajiaz,lynch}@csail.mit.edu

² Northeastern University, Boston, MA 02115, USA
l.su@northeastern.edu

Abstract. We investigate the importance of quorum sensing in the success of house-hunting of emigrating *Temnothorax* ant colonies. Specifically, we show that the absence of the quorum sensing mechanism leads to failure of consensus during emigrations. We tackle this problem through the lens of distributed computing by viewing it as a natural distributed consensus algorithm. We develop an agent-based model of the house-hunting process, and use mathematical tools such as conditional probability, concentration bounds and Markov mixing time to rigorously prove the negative impact of not employing the quorum sensing mechanism on emigration outcomes. Our main result is a high probability bound for failure of consensus without quorum sensing in a two-new-nest environment, which we further extend to the general multiple-new-nest environments. We also show preliminary evidence that appropriate quorum sizes indeed help with consensus during emigrations. Our work provides theoretical foundations to analyze why *Temnothorax* ants evolved to utilize the quorum rule in their house-hunting process.

Keywords: Bio-inspired Algorithms · Distributed Consensus · Stochastic Dynamical Systems.

1 Introduction

Social insect colonies are motivated to move the locations of their nesting site as a functional response to various selected forces, such as colony growth, competition, foraging efficiency, microclimate, nest deterioration, nest quality, parasitism, predation, and seasonality [18]. Through constant adaptation to a changing environment, many social insect species such as ants, termites, and bees have evolved robust algorithms to accomplish the task of collective nest relocation [32]. In this paper, we study one such algorithm observed in colonies of *Temnothorax* ants.

* Corresponding author

Temnothorax ant colonies have many biological constraints: individuals with limited memory and computational power, limited communication, and no central control. Despite that, colonies as a whole can reach various global goals such as nest-site selections and foraging [10]. Their remarkable collective intelligence is not only an interesting problem for biologists, but also inspiring for the computer science community. In particular, from the distributed computing perspective, the collective house-hunting behavior is closely related to the fundamental problem of consensus. Building a theoretical understanding of the key mechanisms in the house-hunting process can thus shed light on the designs of novel distributed consensus algorithms.

Colonies consist of active ants who move the remaining passive workers, the queen, and brood items (immature ants) [25,4]. All workers are female ants. At the beginning of an emigration event, individual active ants independently search for new nest sites. If an ant finds one, she evaluates the site's quality according to various metrics [12,7]. Quality evaluation is relative to the old home nest [3]. If she is not satisfied with the site, she keeps searching. Otherwise if she is satisfied with the site, she returns to the home nest after some time interval that is inversely related to the new nest site quality; during this interval she might continue searching for other new potential nest sites [15,22]. If she returns to the old nest, she recruits another active ant to the site by leading a slow *tandem run* from the old nest to the new site [19,26]. This is done by the leader ant directing the follower ant along a pheromone trail (Fig. 1(a)). Upon arriving at the nest, the follower ant also evaluates the nest's quality independently of the leader ant. Both ants then continue monitoring the quality of the nest and repeat the process of quality estimation, wait interval/continued search, and further recruitment [29].

An ant continues leading tandem runs until she perceives that the new nest's population has exceeded a threshold, or quorum [23]. At this point, she ceases tandem runs and instead starts transporting other ants by picking one up and carrying her from the old home nest to the new nest (Fig. 1(b)). These transports are much faster than tandem runs, and they are largely directed at the passive workers and brood items, hence they serve to quickly move the entire colony to the new nest [22,25]. The transporter rarely drops out of transporting other

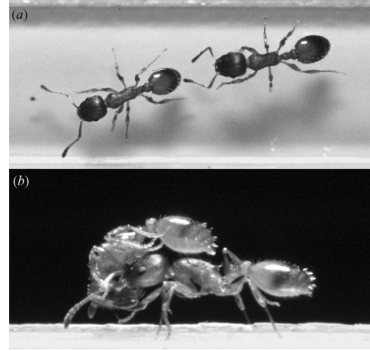


Fig. 1. From [14] (Figure 2). (a) Recruitment via tandem running in the ant of genus *Temnothorax*. The worker at the front is leading a tandem run, and the follower behind is about to signal its presence by tapping with its antennae on the gaster of the leader. (b) Recruitment by transport in *Temnothorax* ants. One worker is simply carrying another quickly to the new nest site. (Both photographs by S. C. Pratt.)

ants, and hence is considered fully committed to the new nest as the colony’s home [29].

Both tandem runs and transports are forms of recruitment to accelerate the emigration process, but the marginal benefits of transports in ensuring consensus remain relatively poorly understood. Previous studies have regarded the quorum sensing mechanism as a way to tune the speed-accuracy trade-off [9,17,16,20,24,31], where a smaller quorum prompts ants to commit sooner (higher speed) to a nest that has accumulated enough population, although that nest could be inferior to another nest that is discovered later in the process (lower accuracy). However, these studies generally equate accuracy with consensus or cohesion [5,6], when all or most ants commit to the same nest. The difference between accuracy and consensus is that the former evaluates the individuals’ ability to choose the best option in the environment, but the latter is concerned only with their ability to agree with each other. The ability to stay in a single group is not only an interesting algorithmic question, but also highly beneficial for the survival of these ant colonies [9,14,6,30]. However, consensus during emigrations has been comparatively understudied. Such studies require examinations of both consensus cases and split cases, and the latter is difficult to induce experimentally. Therefore, in this paper, we conduct one of the first theoretical studies of the role of quorum sensing in emigration consensus.

At the outset, quorum sensing significantly benefits consensus because once enough ants make their choice, that choice is “locked in” and has a higher chance of becoming the final choice. This helps to ensure consensus when there are many choices and the search effort is dispersed. However, a closer look reveals that the quorum size must be carefully chosen. If the quorum size is too large, it would be very unlikely to be reached by any nest; if it is too small, multiple nests will likely reach quorum (a split), incurring significant additional costs in time and risk of exposure of the emigration [1,2,23]. These trade-offs pose the question of whether quorums help with consensus at all. In this paper, we aim to answer this question partially by investigating the probability of emigration consensus *without* the quorum sensing mechanism.

We start by modeling individual active ants as coupled random processes without considering the quorum sensing mechanism. Unlike in most classical distributed algorithms, the ants in our model do not receive initial input preferences, but must determine these preferences through exploration. Another difference is that our consensus requirement exempts a small portion of ants from committing to the same nest. Intuitively, we expect that the distribution of ant states converges to a limiting distribution in the long run. However, due to the probabilistic modeling, there is a non-zero probability that an emigration deviates greatly from this expectation, and this probability depends also on how many ants can be exempted by the requirement. Therefore, detailed calculations are needed to quantify the probability of deviations that satisfy the consensus requirement. Using probability tools such as conditional probability, concentration bounds and Markov mixing time, we then show that without quorum sensing, the probability of consensus is small and decays to zero exponentially fast as the

colony size grows. In addition, we show preliminary evidence that appropriate quorum sizes indeed help with consensus during emigrations.

The rest of the paper is organized as follows. In Section 2, we present our model of individual ants, of the entire colony, and of an execution, for two-nest environments. In Section 3, we formally state the definition of consensus, and the metrics to measure a model’s performance in terms of consensus. In Section 4, we show that with a high probability, emigrations cannot eventually reach consensus without quorum sensing. In Section 5, we extend our results to general k -nest environments where $k > 2$. Then, in Section 6, we consider the addition of the quorum sensing mechanism to the emigration process in two-nest environments, and show simulation results on the quorum sizes that are sufficient for consensus.

2 Model

2.1 Timing Model and the Environment

We divide time into discrete rounds. Individual active ants are modeled as identical probabilistic finite state machines and their dynamics are coupled through recruitment actions, as described later in Section 2.2. Let N denote the total number of active ants in the colony. Note that passive ants, the queen, and brood items can only be transported and have no states. For ease of exposition, in the sequel, by an “ant” we mean an “active ant”. Each ant starts a round with its own state. During each round, ants can perform various state transitions and have new states, before all entering the next round at the same time. Throughout the paper, the state of an ant at round t refers to her state at the end of round t .

The environment contains the original home nest n_0 and two new nests n_1 and n_2 . The new nests n_1 and n_2 have qualities q_1 and q_2 respectively, *relative* to the home nest quality. For the convenience of our analysis, we let $0 < q_2 < q_1 \leq 1$, where a higher value corresponds to a better nest. Each nest is also associated with a *population* that changes from round to round. We use $x_0(t)N$, $x_1(t)N$ and $x_2(t)N$, where $x_0(t) + x_1(t) + x_2(t) = 1$, to denote (active) ant populations in nest n_0 , n_1 and n_2 respectively at the end of round t . Initially, individual ants have no information on q_1 and q_2 .

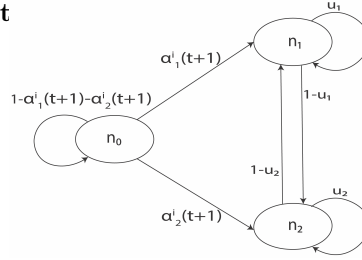


Fig. 2. State transition diagram for ant a_i during round $t + 1$ before/without quorum attainment. $\alpha_1^i(t + 1)$ and $\alpha_2^i(t + 1)$ are composite functions each including the probabilities of an ant taking different paths (independent discovery or tandem running) to transition out of n_0 into n_1 and n_2 , respectively.

2.2 Model of Individual Ants without Quorums

In this subsection, we describe the dynamics of an ant without quorums (a.k.a. without performing state transitions based on seeing a quorum), compactly illustrated in Fig. 2 and Eq. (1) - (6). Though these dynamics are not Markovian

as the state transition of an ant is influenced by other ants during recruitments (tandem runs), we prove (in Section 4) that after a finite time, the state transitions of an ant become independent of the others' states.

Individual state. The set of possible states of an ant is denoted as $\mathcal{S} \triangleq \{n_0, n_1, n_2\}$. Each state n_i refers to the ant being at nest n_i , and thus in the sequel we use “in state n_i ” and “in nest n_i ” interchangeably. Denote the state of ant a_i at the end of round t as $\mathbf{s}_i(t)$ with $\mathbf{s}_i(0) = n_0$ for all a_i , i.e., initially all ants locate at the home nest n_0 .

Transitions out of the home nest. In a round, an ant a_i in n_0 can be recruited by following a tandem run to either n_1 or n_2 . If a_i is not recruited, she discovers nest n_1 or n_2 for the first time through independent discovery with probability $\alpha \in (0, 1/2]$ for either nest and a total discovery probability of 2α . Note that the biological meaning of the parameter α is that it encodes the home nest quality - the higher the home nest quality, the less likely a_i is to search for a new nest during any round t and the smaller α is. Recruitment takes priority over her performing a probabilistic state transition to either n_1 or n_2 through independent discovery.

Formally, at the end of round t , if ant a_i is in n_0 , let $TR_1^i(t+1), TR_2^i(t+1)$ be the event that ant a_i is recruited to n_1 and n_2 respectively during round $t+1$. Let $\tau_1^i(t+1), \tau_2^i(t+1)$ represent their respective conditional probabilities during round $t+1$, i.e.,

$$\mathbb{P}\{TR_m^i(t+1) \mid \mathbf{s}_i(t) = n_0\} = \tau_m^i(t+1), \text{ for } m \in \{1, 2\}.$$

Note that for any ant a_i , the two events are mutually exclusive, and $\tau_1^i(t+1) + \tau_2^i(t+1) \leq 1$. The exact expressions for $\tau_1^i(t+1)$ and $\tau_2^i(t+1)$ are very complex and affect the time that ant a_i transitions out of n_0 , which is an important milestone time for the proofs in this paper. Fortunately, we manage to circumvent calculating the exact expressions of $\tau_1^i(t+1)$ and $\tau_2^i(t+1)$ by deriving a bound on this time using a coupling argument (Proposition 2). We found that this bound was sufficient for proving our main theorem.

With this notation, conditioning on an ant a_i being at state n_0 at time t , the probability of her transitioning to n_1 in the nest round, denoted by $\alpha_1^i(t)$ can be expressed as

$$\begin{aligned} & \mathbb{P}\{\mathbf{s}_i(t+1) = n_1 \mid \mathbf{s}_i(t) = n_0\} \triangleq \alpha_1^i(t+1) \\ &= \mathbb{P}\{TR_1^i(t+1) \mid \mathbf{s}_i(t) = n_0\} \\ & \quad + \mathbb{P}\{\mathbf{s}_i(t+1) = n_1 \mid (\mathbf{s}_i(t) = n_0 \wedge \neg(TR_1^i(t+1) \vee TR_2^i(t+1)))\} \\ & \quad \cdot \mathbb{P}\{\neg(TR_1^i(t+1) \vee TR_2^i(t+1)) \mid \mathbf{s}_i(t) = n_0\} \\ &= \tau_1^i(t+1) + \alpha(1 - \tau_1^i(t+1) - \tau_2^i(t+1)), \end{aligned} \tag{1}$$

where α can be formally expressed as

$$\alpha = \mathbb{P}\{\mathbf{s}_i(t+1) = n_1 \mid (\mathbf{s}_i(t) = n_0 \wedge \neg(TR_1^i(t+1) \vee TR_2^i(t+1)))\}$$

. It is easy to see that $\alpha_1^i(t+1)$ sums up the probability of her getting recruited to n_1 and the probability of independent discovery of n_1 in the case that she

does not get recruited to either n_1 or n_2 . Similarly, we define $\alpha_2^i(t+1)$ as the probability of her transitioning to n_2 during round $t+1$, i.e.,

$$\begin{aligned} & \mathbb{P}\{\mathbf{s}_i(t+1) = n_2 \mid \mathbf{s}_i(t) = n_0\} \\ & \triangleq \alpha_2^i(t+1) = \tau_2^i(t+1) + \alpha(1 - \tau_1^i(t+1) - \tau_2^i(t+1)). \end{aligned} \quad (2)$$

Correspondingly,

$$\mathbb{P}\{\mathbf{s}_i(t+1) = n_0 \mid \mathbf{s}_i(t) = n_0\} = 1 - \alpha_1^i(t+1) - \alpha_2^i(t+1). \quad (3)$$

Transitions between new nests.

When $\mathbf{s}_i(t) = n_m$ for $m \in \{1, 2\}$, at the beginning of round $t+1$, with probability $(1 - u_m)$, ant a_i chooses to search her environment and discover the new nest she is not currently at, i.e.,

$$\mathbb{P}\{\mathbf{s}_i(t+1) = n_{3-m} \mid \mathbf{s}_i(t) = n_m\} = 1 - u_m, \quad \forall m \in \{1, 2\}; \quad (4)$$

with probability u_m , ant a_i tries to recruit another ant from state n_0 through a tandem run and comes back to n_m , i.e.,

$$\mathbb{P}\{\mathbf{s}_i(t+1) = n_m \mid \mathbf{s}_i(t) = n_m\} = u_m, \quad \forall m \in \{1, 2\}. \quad (5)$$

If there is no more ant left in n_0 to recruit, the leader ant a_i simply returns to nest n_m without recruiting another ant. The recruiting probability u_m is determined by the quality of new nest n_m as

$$u_m \triangleq \frac{1}{1 + \exp(-\lambda q_m)}, \quad \forall m \in \{1, 2\}, \quad (6)$$

where the parameter $\lambda > 0$ represents the noise level of individual decision making to evaluate the quality of a nest n_m for $m \in \{1, 2\}$. A larger λ means a less noisy decision rule, and thus a higher probability of recruitment to the superior site n_m . Also note that $u_1, u_2 \in [0.5, 1]$ and $u_1 > u_2$.

Our choice of the sigmoid function is rooted in empirical evidence. The decision making mechanism for individual ant recruitment has been shown by a number of experimental and modeling studies to be both quality-dependent [15, 24, 25, 21] and threshold-based (individuals compare the perceived nest quality to a fixed threshold) [28, 27]. The sigmoid function we chose here is thus a common choice that incorporates both dependencies into the modeling of noisy individual decision making. Intuitively, when n_m has a quality higher than that of n_0 's, n_m is the better choice and it is beneficial for ants to recruit to it. When a nest n_m is strongly superior to n_0 , i.e., the quality difference surpasses a threshold, the probability of an individual ant recruiting to n_m should thus be very high (close to 1 in our model). The sigmoid function is a “smooth” representation of this threshold-based rule. On the other hand, when the quality difference is small, the probability of recruitment has stronger dependencies on the quality difference. This case is modeled by a near-linear segment in the sigmoid function.

Remark 1 (Non-markovian dynamics of an individual ant). The state $\mathbf{s}_i(t)$ of any individual ant a_i during round t has dependencies on 1) her own state in the previous round $\mathbf{s}_i(t-1)$, and 2) the recruitment actions of other ants.

2.3 Dynamics of the Entire Colony

We now describe what happens in an arbitrary execution, or emigration. Throughout the paper, we use “an execution” and “an emigration” interchangeably, referring to an emigration event.

Let $\mathbf{s}(t) = \{\mathbf{s}_1(t), \dots, \mathbf{s}_N(t)\}$ for $t = 0, 1, \dots$ denote the random process of the entire colony state, represented by a vector of dimension N that stacks the states of individual ants in the colony. Although $\mathbf{s}_i(t)$ for any i is not Markovian, it is easy to see that $\mathbf{s}(t)$ is a Markov chain, since for any tandem leader in round t , the choice of a follower only depends on $\mathbf{s}(t-1)$ and not on any history prior to round $t-1$. An emigration starts from round 1, with $\mathbf{s}_i = n_0$ for all $i = 1, \dots, N$. During each round, each ant not in n_0 performs one state transition in random order, followed by each ant in n_0 performing one state transition in random order. At the beginning of a round t , each ant has her own state $\mathbf{s}_i(t-1)$ and the colony has state $\mathbf{s}(t-1)$. If at the beginning of round t she is in nest n_1 or n_2 , respectively, the population at that nest at the beginning of round t is also available to a_i . During a round t , each individual ant performs one state transition according to the individual models in Section 2.2, which results in a transition of the colony state as well during this round. At the end of round t , each ant has a new state $\mathbf{s}_i(t)$ and the colony has state $\mathbf{s}(t)$. All ants then enter the next round $t+1$ with their new states.

3 The Consensus Problem

Here we define what it means for an emigration to reach consensus. We say that an emigration has reached Δ -consensus (where $\Delta \in [0, \frac{1}{2}]$) if there exists \tilde{t} such that for all $t \geq \tilde{t}$ and a nest $m \in \{1, 2\}$, the proportion of the population at nest n_m at time t is greater than or equal to $1 - \Delta$, i.e., $x_m(t) \geq (1 - \Delta)$.

The metric to evaluate a model’s performance is the *consensus probability* C , which is the probability that an emigration reaches consensus as defined above.

Remark 2. Note that Δ represents the proportion of ants that can be *exempted* from the consensus requirement. We can see that the smaller Δ is (lowest value is 0), the larger $(1 - \Delta)N$ is, and hence the more ants are required for an emigration to reach consensus. In other words, the smaller Δ is, the more “strict” the consensus metric is and the more challenging it is for an emigration to reach consensus.

4 Failure of Consensus in Two-Nest Environments

In this section, we explore colony emigration behavior *only* with individual transition rules and tandem runs defined above (i.e., without quorum sensing). Equivalently, we consider the case where the quorum size is N , so that the quorum sensing mechanism never has any effect. We show an upper bound on the consensus probability C for a given Δ and colony size N . This upper bound decreases to 0 exponentially fast as $N \rightarrow \infty$.

Next we introduce two quantities, denoted by H and π^* , that will be used in the statement of our main result. It is easy to see from Eq. (4) and (5) that if an ant a_i jumps out of the home nest n_0 at some time, then from that time onward, the state transition of a_i becomes Markovian and is governed by the following transition matrix

$$H = \begin{bmatrix} u_1 & 1 - u_1 \\ 1 - u_2 & u_2 \end{bmatrix}. \quad (7)$$

The transition in H is also illustrated in Fig. 4. It can also be seen (which we will formally show later) that the state of each ant has an identical limiting distribution, denoted by $\pi^* \triangleq \frac{1}{2 - u_1 - u_2} [1 - u_2, 1 - u_1] \in \mathbb{R}^2$, with support on $\{n_1, n_2\}$ only.

Theorem 1. *For any $\Delta \in [0, 1 - \pi^*(n_1)]$, let $\epsilon_0 = \frac{1 - \pi^*(n_1) - \Delta}{2} > 0$. Then it holds that*

$$\mathbb{P} \left\{ \sum_{i=1}^N \mathbb{1}\{\mathbf{s}_i(t) = n_1\} \geq (\pi^*(n_1) + 2\epsilon_0)N = (1 - \Delta)N \right\} \leq 2 \exp \left(-\frac{\epsilon_0^2 N}{2} \right),$$

for any $t > \left(\frac{1}{\ln(1 - 2\alpha)} + \frac{1}{\ln(1 - R(H))} \right) \ln \frac{\epsilon_0}{2}$, where $R(H) = 2 - u_1 - u_2$ is Dobrushin's coefficient of ergodicity ([11, Chapter 6.2] and Appendix A) of H .

Remark 3. Theorem 1 is stated for n_1 . A similar result holds for n_2 . Theorem 1 says that for any t greater than $\left(\frac{1}{\ln \beta} + \frac{1}{\ln(1 - R(H))} \right) \ln \frac{\epsilon_0}{2}$, the probability of $x_1(t)$ reaching $(1 - \Delta)$ is upper bounded by $2 \exp \left(-\frac{\epsilon_0^2 N}{2} \right)$. Thus, the total consensus probability C for the given Δ is upper bounded by $4 \exp \left(-\frac{\epsilon_0^2 N}{2} \right)$, which decreases to 0 exponentially fast as N increases. It is worth noting that real ant colonies often need Δ to be very small or even zero for survival. From the theorem expression, we can see that the smaller Δ is, i.e., the more stringent the consensus, the lower is the upper bound of the consensus probability. Therefore, Theorem 1 implies that extra mechanisms, such as the quorum rule are necessary to help the emigration reach consensus.

Later in Section 5, we also show that the proofs in this section and related results can easily extend to environments with multiple nests.

4.1 Analysis of Main Result

Despite the fact that the dynamics of the entire ant colony is a Markov chain, analyzing this Markov chain is highly non-trivial because the state is quite involved and the state space is huge – it contains all the possible partitions of ants into three groups, with each group representing one nest as the state of an individual ant. In this proof section we analytically show that despite the fact

that the emigration behaviors of individual ants are *interactive*, the dynamics of any individual ant are independent of other ants shortly after she leaves the original home nests either through discovery or through recruitment. Moreover, we show that this independence manifests itself in a non-trivial way after a few rounds – suggesting that a large portion of ants quickly rely only on individual intelligence. Then we show that this independence is harmful to realizing social cohesion.

Several intermediate results are derived in proving Theorem 1. The connections of the supporting lemmas and corollaries with respect to Theorem 1 are shown in Fig. 3.

Definition 1. For each $i \in [N]$, define random variable $T_i^1 \triangleq \inf\{t : \mathbf{s}_i(t) \neq n_0\}$ as the first round at the beginning of which ant a_i has transitioned out of the n_0 state in any arbitrary execution of the emigration.

Remark 4. It can be shown that T_i^1 is finite with probability 1 (Appendix A, Prop. 4). It follows immediately from Definition 1 that $\mathbb{P}\{\mathbf{s}_i(t) = n_0 \mid t \geq T_i^1\} = 0$ for any ant a_i .

It turns out that ant a_i 's state transitions become independent of other ants after T_i^1 , the time that a_i leaves n_0 , formally stated in the following proposition.

Proposition 1. For every $i, j \in [N], i \neq j$ and every $t > T_i^1$, the state transitions of ant a_i are independent from a_j , i.e.,

$$\begin{aligned} \mathbb{P}\{\mathbf{s}_i(t+1) = s'_1 \mid (\mathbf{s}_i(t) = s_1) \wedge (\mathbf{s}_j(t) = s_2) \wedge (t > T_i^1)\} \\ = \mathbb{P}\{\mathbf{s}_i(t+1) = s'_1 \mid (\mathbf{s}_i(t) = s_1) \wedge (t > T_i^1)\}, \end{aligned}$$

where $s_1, s_2, s'_1 \in \mathcal{S}$ and $s'_1 \neq n_0$.

The next proposition is devoted to showing that after a few rounds, many ants have left the home nest n_0 . Consider N random indicator variables $\mathbb{1}\{T_i^1 > t\}$ for any t , each variable taking values in the $\{0, 1\}$. Using stochastic dominance and Hoeffding's inequality [13] (also Appendix A), we show a high probability upper bound on the number of ants still in n_0 at round t . Here stochastic dominance is used to tackle the challenges caused by the dependency among the N indicator random variables.

Proposition 2. Let $\beta \triangleq 1 - 2\alpha$. For $t \geq 1$ and any number $d \in [0, 1]$, it holds that

$$\mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{T_i^1 > t\} < N(\beta^t + d)\right\} > 1 - \exp(-2Nd^2),$$

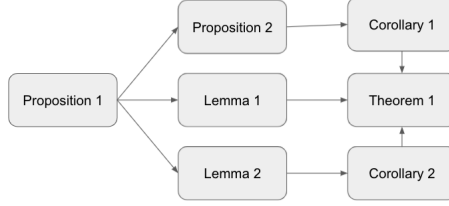


Fig. 3. Flowchart of the proofs.

i.e., with a probability of at least $(1 - \exp(-2Nd^2))$, the number of ants staying at home nest beyond time t is at most $N(\beta^t + d)$.

Corollary 1. For any given $\epsilon \in (0, 1)$, for any $t \geq \log_\beta(\frac{\epsilon}{2})$, it holds that

$$\mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{T_i^1 > t\} < \epsilon N\right\} > 1 - \exp(-N\epsilon^2/2).$$

In other words, with a probability of at least $(1 - \exp(-N\epsilon^2/2))$, at most ϵN ants remain in the home nest n_0 after round $\log_\beta(\frac{\epsilon}{2})$.

Next, we show that every ant a_i has an identical limiting distribution. Towards this, we first show that every ant a_i that has transitioned out of n_0 has the same limiting distribution. Furthermore, we show that all ants eventually transition out of n_0 and thus all ants share the same limiting distribution. The proof of Lemma 1 uses the quantity $Q(t)$, defined as

$$Q(t) \triangleq \{a_i : s_i(t) \neq n_0\} \quad (8)$$

which is a random variable representing the set of ants that have transitioned out of n_0 by the end of round t , in an arbitrary emigration. $Q(t)$ is thus a function of an execution. It is easy to see that w.r.t. this emigration, $Q(t-1) \subseteq Q(t)$ for any $t \geq 1$.

Lemma 1. For each a_i , its limiting distribution, denoted by π_i , is well-defined, and can be expressed as

$$\pi_i \triangleq \frac{1}{2 - u_1 - u_2} [1 - u_2, 1 - u_1]. \quad (9)$$

For ease of exposition, we define $\pi^* = \pi_i$. From Lemma 1 it can be seen that the probability ratio $\frac{\pi^*(n_1)}{\pi^*(n_2)} = \exp(\lambda(q_1 - q_2))$ is very sensitive to the nest quality gap $(q_1 - q_2)$ and λ .

It turns out that for t large enough, any ant that has transitioned out of n_0 has state distributions “close” to the stationary distribution π^* , formally stated next.

Lemma 2. For any ant a_i , let $\pi_{i,t}$ denote the probability distribution of her state over the possible states depicted in Fig. 4 at time $t \geq T_i^1$. Then for any number of rounds $\ell > 0$, it holds that

$$\|\pi_{i,T_i^1+\ell} - \pi^*\|_1 \leq 2(1 - R(H))^\ell.$$

Using Lemma 2, the following corollary immediately follows:

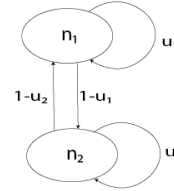


Fig. 4. State transition diagram for individual ants after they leave n_0 , before/without quorum attainment.

Corollary 2. Fix any $\delta \in (0, 1)$. For any ant a_i and $t > T_i^1 + \ell$, where $\ell \triangleq \log_{(1-R(H))} \frac{\delta}{2}$, it holds that

$$\|\pi_{i,t} - \pi^*\|_1 \leq \delta.$$

Combined with Corollary 1, we are now ready to prove Theorem 1.

Proof of Theorem 1

We first give the intuition and a proof sketch to show an upper bound on the probability of the population at n_1 being higher than a certain number C_0 , for t large enough.

We break down the problem into two cases. In the first case, by a certain milestone-round k_1 , the number of ants that have transitioned out of n_0 is low. In the second case, that number is high. Now, by applying concentration bounds, we show that the first case has a low probability. We thus subsequently focus on analyzing the second case which has a high probability. From Corollary 2 we know that after a certain number k_2 of rounds, most of the ants that have left n_0 will have distributions that are very close to the limiting distribution π^* . Thus, at any round $t \geq k_1 + k_2$, with high probability, the proportion of ants in n_1 is also close to $\pi^*(n_1)$ among ants that have left n_0 (at most N ants). In other words, after $k_1 + k_2$ rounds the probability of n_1 's population being much higher than $\pi^*(n_1)N$ should be quite low. Summing up the bounds for the first and second cases gives us an overall upper bound on this probability, proving the theorem.

For ease of exposition, let $B_i(t) = \mathbb{1}\{\mathbf{s}_i(t) = n_1\}$ for each $i \in [N]$ and $t \geq 0$. Let C_0 be an arbitrary positive number, $C_0 \in [0, N]$. Let $C_1 = (1 - \epsilon_0)N$. Recall that $\beta = 1 - 2\alpha$.

$$\begin{aligned} \mathbb{P} \left\{ \sum_{i=1}^N \mathbb{1}\{\mathbf{s}_i(t) = n_1\} \geq C_0 \right\} &= \mathbb{P} \left\{ \sum_{i=1}^N B_i(t) \geq C_0 \right\} \\ &= \mathbb{P} \left\{ \sum_{i=1}^N B_i(t) \geq C_0 \mid \left| Q(\log_\beta \frac{\epsilon_0}{2}) \right| < C_1 \right\} \mathbb{P} \left\{ \left| Q(\log_\beta \frac{\epsilon_0}{2}) \right| < C_1 \right\} \\ &\quad + \mathbb{P} \left\{ \sum_{i=1}^N B_i(t) \geq C_0 \mid \left| Q(\log_\beta \frac{\epsilon_0}{2}) \right| \geq C_1 \right\} \mathbb{P} \left\{ \left| Q(\log_\beta \frac{\epsilon_0}{2}) \right| \geq C_1 \right\} \\ &\leq \mathbb{P} \left\{ \left| Q(\log_\beta \frac{\epsilon_0}{2}) \right| < C_1 \right\} + \mathbb{P} \left\{ \sum_{i=1}^N B_i(t) \geq C_0 \mid \left| Q(\log_\beta \frac{\epsilon_0}{2}) \right| \geq C_1 \right\}. \quad (10) \end{aligned}$$

We bound the two terms in the RHS of Eq.(10) separately.

Bounding the 1st term: For any $t \geq \log_\beta \frac{\epsilon_0}{2}$, we have

$$\begin{aligned}
\mathbb{P}\{|Q(t)| < C_1\} &= \mathbb{P}\{|Q(t)| < (1 - \epsilon_0)N\} \\
&= \mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{\mathbf{s}_i(t) \neq n_0\} < (1 - \epsilon_0)N\right\} \\
&= \mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{T_i^1 \leq t\} < (1 - \epsilon_0)N\right\} \\
&= \mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{T_i^1 > t\} > \epsilon_0 N\right\} \\
&\leq \exp\left(-\frac{\epsilon_0^2 N}{2}\right),
\end{aligned}$$

where the last inequality follows from Corollary 1.

Bounding the 2nd term: Note that

$$\sum_{i=1}^N B_i(t) = \sum_{a_i \in Q(t)} B_i(t) + \sum_{a_i \notin Q(t)} B_i(t).$$

It is easy to see that

$$\sum_{a_i \notin Q(t)} B_i(t) = 0. \quad (11)$$

In addition, we have

$$\begin{aligned}
&\mathbb{P}\left\{\sum_{a_i \in Q(t)} B_i(t) - \sum_{a_i \in Q(t)} \mathbb{E}[B_i(t)] \geq \epsilon_0 |Q(t)| \mid |Q(t)| \geq (1 - \epsilon_0)N\right\} \\
&= \mathbb{P}\left\{\sum_{a_i \in Q(t)} B_i(t) - \sum_{a_i \in Q(t)} \pi_{i,t}(n_1) \geq \epsilon_0 |Q(t)| \mid |Q(t)| \geq (1 - \epsilon_0)N\right\} \\
&\leq \exp(-2|Q(t)|\epsilon_0^2) \\
&\leq \exp(-2(1 - \epsilon_0)\epsilon_0^2 N).
\end{aligned}$$

Conditioning on $|Q(\log_\beta \frac{\epsilon_0}{2})| \geq (1 - \epsilon_0)N$, from Corollary 2, we know that for each $a_i \in Q(\log_\beta \frac{\epsilon_0}{2})$, for any $t > \log_\beta \frac{\epsilon_0}{2} + \ell$, where $\ell = \log_{(1-R(H))} \frac{\epsilon_0}{2}$, it holds that $\pi_{i,t}(n_1) \leq \pi^*(n_1) + \epsilon_0$. Hence we get

$$\begin{aligned}
\sum_{a_i \in Q(t)} \pi_{i,t}(n_1) + \epsilon_0 |Q(t)| &\leq (\pi^*(n_1) + \epsilon_0) |Q(t)| + \epsilon_0 |Q(t)| \\
&\leq (\pi^*(n_1) + 2\epsilon_0) N.
\end{aligned}$$

Thus,

$$\begin{aligned}
& \mathbb{P} \left\{ \sum_{a_i \in Q(t)} B_i(t) \geq (\pi^*(n_1) + 2\epsilon_0) N \right\} \\
& \leq \mathbb{P} \left\{ \sum_{a_i \in Q(t)} B_i(t) - \sum_{a_i \in Q(t)} \mathbb{E}[B_i(t)] \geq \epsilon_0 |Q(t)| \mid |Q(t)| \geq (1 - \epsilon_0)N \right\} \\
& \leq \exp(-2(1 - \epsilon_0)\epsilon_0^2 N). \tag{12}
\end{aligned}$$

Combining Eq. (11) and (12), we conclude that

$$\mathbb{P} \left\{ \sum_{i=1}^N B_i(t) \geq (\pi^*(n_1) + 2\epsilon_0) N \mid |Q(t)| \geq (1 - \epsilon_0)N \right\} \leq \exp(-2(1 - \epsilon_0)\epsilon_0^2 N).$$

Combining the probability bounds on the first and second terms of Thm. 1, we have

$$\begin{aligned}
& \mathbb{P} \left\{ \sum_{i=1}^N \mathbb{1}\{\mathbf{s}_i(t) = n_1\} \geq (\pi^*(n_1) + 2\epsilon_0) N \right\} \\
& \leq \exp(-2(1 - \epsilon_0)\epsilon_0^2 N) + \exp\left(-\frac{\epsilon_0^2 N}{2}\right) \\
& \leq 2 \exp\left(-\frac{\epsilon_0^2 N}{2}\right) \quad \text{as } \epsilon_0 \in (0, 1/2),
\end{aligned}$$

proving Theorem 1.

5 Extension: Failure of Consensus in More-Nest Environments

Both the results on asymptotic independence and its negative impact presented in Section 4 can be extended to the general k -new-nest environments where $k > 2$. On a high level, the necessary additions to the individual transition model (Fig. 2) are: 1) a new state for each new nest, each similar to the n_1 and n_2 , 2) all new nests can exchange ants with each other, and 3) all new nests can receive ants from n_0 through recruitment or discovery. The model for timing, environment, and execution of the whole colony remain the same as the two-nest case, where n_1 has the highest quality. After adjusting quantities H and π^* , one can derive results similar to Theorem 1: without quorum sensing, the probability of consensus can be arbitrarily low. We detail these changes below in this section.

Fig. 5 shows the transition diagram for an individual ant before/without her seeing a quorum at any nest, and Eq. (13)-(16) define transition probabilities among the four states. Similar to the two-nest case, $\mathbb{P}\{TR_i^i(t+1)\} = \tau_i^i(t+1)$

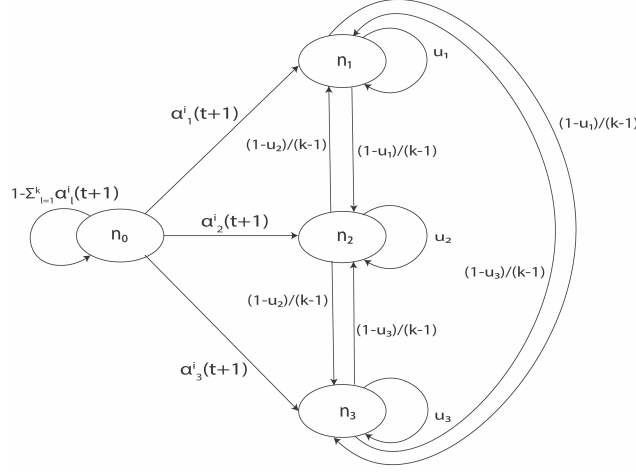


Fig. 5. State transition diagram for ant a_i during round $t + 1$ in a k -nest environment before/without quorum attainment. Probabilities $\alpha_l^i(t + 1), l \in [1, k]$ are composite functions each including the probabilities of an ant taking different paths (independent discovery or tandem running) to transition out of n_0 into n_l . Compared to Fig. 2, this figure shows the addition of one more new nest n_3 ; any more new nests can be added in the same way.

for each $l \in [1, k]$ is defined as the probability of the event that ant a_i transitions from n_0 to n_l during round $t + 1$ by following a tandem run. Fig. 5 displays only the addition of a third new nest, n_3 , and any more new nest can be added in the same way. The addition of n_3 requires that during round t , an ant at n_0 transitions to n_3 with probability $\alpha_3(t)$; an ant at n_3 stays in n_3 with probability u_3 ; and an ant at a new nest l transitions to any other new nest $m \neq l$ with transition probability $\frac{1-u_l}{k-1}$.

$$\mathbb{P}\{s_i(t+1) = n_l \mid s_i(t) = n_0\} = \alpha_l^i(t) \text{ for } l \in [1, k] \quad (13)$$

$$\mathbb{P}\{s_i(t+1) = n_0 \mid s_i(t) = n_0\} = 1 - \sum_{l=1}^k \alpha_l^i(t) \quad (14)$$

$$\mathbb{P}\{s_i(t+1) = n_l \mid s_i(t) = n_l\} = u_l \text{ for } l \in [1, k] \quad (15)$$

$$\mathbb{P}\{s_i(t+1) = n_m \mid s_i(t) = n_l\} = \frac{1-u_l}{k-1} \text{ for } l, m \in [1, k] \text{ and } m \neq l \quad (16)$$

where

$$\begin{aligned}
\alpha_l^i(t) &\triangleq \mathbb{P} \{TR_l^i(t)\} \\
&+ \mathbb{P} \{ \mathbf{s}_i(t+1) = n_l \mid (\mathbf{s}_i(t) = n_0 \wedge \neg(TR_1^i(t) \vee TR_2^i(t) \vee \dots \vee TR_k^i(t))) \} \\
&\cdot \mathbb{P} \{ \neg(TR_1^i(t) \vee TR_2^i(t) \vee \dots \vee TR_k^i(t)) \mid \mathbf{s}_i(t) = n_0 \} \\
&= \tau_l^i(t) + \alpha(1 - \sum_{l=1}^k \tau_l^i(t)), \text{ for } l \in [1, k], \\
u_l &\triangleq \frac{1}{1 + \exp(-\lambda_{q_l})} \text{ for } l \in [1, k].
\end{aligned}$$

The two quantities used in the main theorem for a k -nest environment, H and π^* , are also different, as shown below.

- H , a $k \times k$ transition matrix of an arbitrary ant a_i 's state \mathbf{s}_i after she transitions out of n_0 , as specified in Eq. (17).
- $\pi^* \in \mathbb{R}^k$, a vector representing the limiting distribution of an arbitrary ant a_i (Eq. (18)). The l -th element is the limiting distribution of state n_l , for $l \in [1, k]$.

$$H = \begin{bmatrix} u_1 & \frac{1-u_1}{k-1} & \frac{1-u_1}{k-1} & \frac{1-u_1}{k-1} & \dots & \frac{1-u_1}{k-1} \\ \frac{1-u_2}{k-1} & u_2 & \frac{1-u_2}{k-1} & \frac{1-u_2}{k-1} & \dots & \frac{1-u_2}{k-1} \\ \frac{1-u_3}{k-1} & \frac{1-u_3}{k-1} & u_3 & \frac{1-u_3}{k-1} & \dots & \frac{1-u_3}{k-1} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \frac{1-u_k}{k-1} & \frac{1-u_k}{k-1} & \frac{1-u_k}{k-1} & \frac{1-u_k}{k-1} & \frac{1-u_k}{k-1} & u_k \end{bmatrix}. \quad (17)$$

Solving the equation system $\pi_i = \pi_i H$, we also obtain that

$$\pi^*(l) = \frac{\prod_{m \in [1, k], m \neq l}^k (1 - u_m)}{\sum_{w=1}^k \left(\prod_{m \in [1, k], m \neq w}^k (1 - u_m) \right)}, \text{ for } l \in [1, k]. \quad (18)$$

Main Theorem for k -Nests

Theorem 2. For any $\Delta \in [0, 1 - \pi^*(n_1)]$, let $\epsilon_0 = \frac{1 - \pi^*(n_1) - \Delta}{2} > 0$. Then it holds that

$$\mathbb{P} \left\{ \sum_{i=1}^N \mathbb{1} \{ \mathbf{s}_i(t) = n_1 \} \geq (\pi^*(n_1) + 2\epsilon_0) N = (1 - \Delta) N \right\} \leq 2 \exp \left(-\frac{\epsilon_0^2 N}{2} \right),$$

for any $t > \left(\frac{1}{\ln(1-k\alpha)} + \frac{1}{\ln(1-R(H))} \right) \ln \frac{\epsilon_0}{2}$, where $R(H)$ is Dobrushin's coefficient of ergodicity ([11, Chapter 6.2] and Appendix A) of H .

Remark 5. Theorem 2 is stated for n_1 . A similar result holds for n_l for $l > 1$. Like in the two-nest case, Theorem 2 again implies that extra mechanisms, such as the quorum rule are necessary to help the emigration reach consensus.

6 Consensus With Quorum Sensing in Two-Nest Environments

An important work in progress is analyzing the probability of consensus when the quorum rule is in effect. In this section, we show as a work in progress the addition of the quorum sensing mechanism to our model, and our current results on the quorum sizes that are sufficient for consensus of average emigrations in two-nest environments.



Fig. 6. State transition diagram for individual ants committed to n_1 and n_2 , on the left and right, respectively.

Note that the dynamics shown in Fig. 2 are also accurate here before an ant a_i sees a quorum for the first time at either nest. Thus, she starts her transitions according to Fig. 2 before seeing any quorum. The evaluation of whether n_m has reached quorum happens whenever a_i is in n_m at the beginning of a round t . Before she performs any transitions during round t , she compares the nest population to a quorum size, if a_i has not yet seen a quorum at n_m (or at any other nest). Once she detects that the population is at least as high as the quorum size, she becomes “committed” to n_m . After that, she no longer monitors the nest’s population. We model an ant’s commitment by disallowing her to transition out of n_m . This means she has to perform a transport action and stay in the n_m state at any round after n_m ’s quorum attainment. As a result, once a nest reaches the quorum, it never drops out of the quorum and every ant that transitions to that nest gets “stuck” in that nest. We thus model a “committed” ant with a separate Markov chain that essentially only has one possible state, as shown in Fig. 6 and Eq. (19)-(22). For a committed ant a_i , let n_m be the nest that she is committed to where $m \in \{1, 2\}$. Then the other new nest she is not committed to is n_{3-m} .

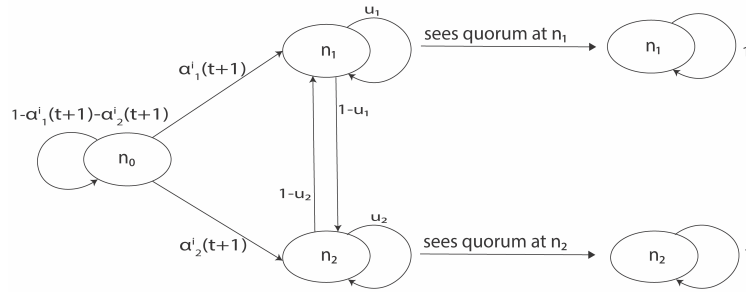


Fig. 7. State transition diagram for ant a_i during round $t + 1$ with the quorum sensing mechanism. She first starts transitioning according to the left part of the figure, identical to Fig. 2. Then once she sees a quorum at either n_1 and n_2 (but not both), she commits to that nest and can only stay in that nest, as shown on the right part of the figure, identical to Fig. 6.

$$\mathbb{P}\{s_i(t+1) = n_m \mid s_i(t) = n_m\} = 1 \quad (19)$$

$$\mathbb{P}\{s_i(t+1) = n_{3-m} \mid s_i(t) = n_m\} = 0 \quad (20)$$

$$\mathbb{P}\{s_i(t+1) = n_m \mid s_i(t) = n_{3-m}\} = 0 \quad (21)$$

$$\mathbb{P}\{s_i(t+1) = n_{3-m} \mid s_i(t) = n_{3-m}\} = 0. \quad (22)$$

Individual Model With Quorums We show the full model in Fig. 7. The addition of transporting as a possible recruitment method thus has two impacts in the full model:

- An ant a_i in n_0 can get recruited by being transported to either n_1 or n_2 , in addition to following a tandem run.
- an ant a_i in either state n_1 or n_2 choosing to stay in the same state tries to recruit another ant from state n_0 through a tandem run if the quorum is not reached (Fig. 2, Eq. (5)), or through a transport otherwise (Fig. 6, Eq. (19)). Whether the recruitment is successful or not still has no effect on a_i 's own state transitions during this round. Otherwise, if she does not recruit, she searches her environment and discovers the new nest she is not currently at (Eq. (4)).

It still holds that during any given round t , if an ant a_i at n_0 does not get recruited, her transitions are Markovian and independent (Fig. 2, Fig. 6). The whole colony dynamics are the same as shown in Section 2.3 and the whole colony state retains its Markovian properties.

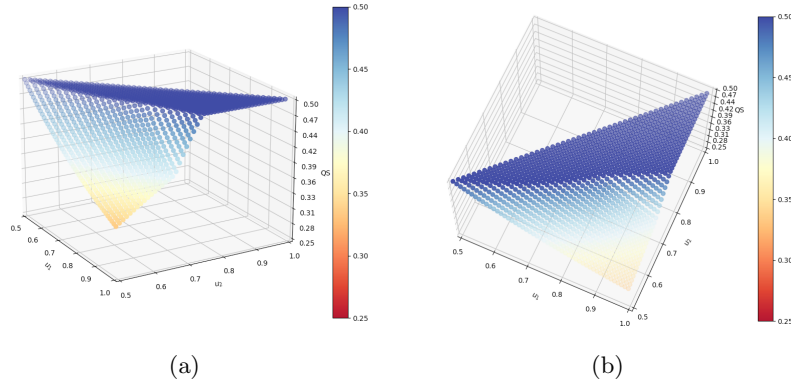


Fig. 8. 3D plots demonstrating quorum sizes that are sufficient for consensus, when $\alpha \leq \frac{1}{3}$. Views from two angles.

Current Work: In our work in progress, through theoretical analysis and simulation work, we are striving to derive quorum sizes that are sufficient for consensus. Our preliminary results in Fig. 8 show such quorum sizes for two-nest environments. In these emigrations, we enforce that $\Delta = 0$ to model the most challenging requirement of consensus. In Fig. 8, for the full ranges of u_1 and u_2 in the frequent case that $\alpha < \frac{1}{3}$, we visualize the quorum sizes (QS) in the range $[0.25, 0.5]$ that are expected to lead to consensus. The desirable values of the quorum size show general consistency with experimental findings of the observed quorum size employed by *Temnothorax* ant colonies [8,22]. However, we are still working on deriving the mathematical expressions for quorum sizes that are sufficient for consensus, as well as on extending these results to k -nest environments ($k > 2$). We plan to show all related details of this effort in a follow-up manuscript.

7 Discussion and Future Work

In this paper, we used analytical tools to show that without quorum sensing, the collective nest site selection process by *Temnothorax* ants has a limited probability to reach consensus. And this probability can be arbitrarily low for a colony size arbitrarily large. Conversely, we obtain a high probability bound for failure of consensus. Without quorum sensing, the only form of recruitment, tandem runs, does speed up the emigration process, but our results show that emigrations would still have a high probability of splitting among multiple new sites, imposing significant risks to the colony’s survival. We first analyze a model of a two-new-nest environment, and then extend our results to environments with more nests. Our results provide insights into the importance of extra mechanisms, such as the quorum sensing mechanism, for emigrations to reach consensus in an unpredictable environment with multiple nests.

In this paper we also provided a preview of an important work in progress investigating how different quorum sizes influence emigration outcomes if quorum sensing is involved, in two-nest environments. Further extensions in this direction are to apply similar analytical methods to the general environment with the addition of quorum sensing to gain insights on how the number of nests and their qualities might influence the desirable values for the quorum size, with the goal to avoid splits, or to ensure consensus, or with an objective involving a specific degree or probability of consensus.

Additionally, another future work direction is to make our model more bioplausible. Specifically, our model does not consider the very small probability that committed ants “drop out” of the nest they are committed to, and go back to searching. Adding this into the model could make it biologically more realistic.

Finally, one more way to strengthen our theoretical results is by adding a time bound metric to our consensus problem. Our current consensus metric, the consensus probability C , only requires that at least $(1 - \Delta)N$ ants keep staying at either n_1 or n_2 after a finite number of rounds. By adding a time bound metric

as well, we would be able to better characterize the consensus probability (even if lower than a given C) of an emigration by a certain time t .

Acknowledgements. J. Zhao and N. Lynch are supported by NSF Awards CCF-2003830, CCF-1461559 and CCF-0939370.

References

1. Doering, G.N., Pratt, S.C.: Queen location and nest site preference influence colony reunification by the ant *temnothorax rugatulus*. *Insectes Sociaux* **63**(4), 585–591 (2016) [3](#)
2. Doering, G.N., Pratt, S.C.: Symmetry breaking and pivotal individuals during the reunification of ant colonies. *Journal of Experimental Biology* **222**(5) (2019) [3](#)
3. Doran, C., Newham, Z.F., Phillips, B.B., Franks, N.R.: Commitment time depends on both current and target nest value in *temnothorax albipennis* ant colonies. *Behavioral Ecology and Sociobiology* **69**(7), 1183–1190 (2015) [2](#)
4. Dornhaus, A., Holley, J.A., Pook, V.G., Worswick, G., Franks, N.R.: Why do not all workers work? colony size and workload during emigrations in the ant *temnothorax albipennis*. *Behavioral Ecology and Sociobiology* **63**(1), 43–51 (2008) [2](#)
5. Franks, N.R., Dechaume-Moncharmont, F.X., Hanmore, E., Reynolds, J.K.: Speed versus accuracy in decision-making ants: expediting politics and policy implementation. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* (1518), 845–852 (03 2009) [3](#)
6. Franks, N.R., Dornhaus, A., Fitzsimmons, J.P., Stevens, M.: Speed versus accuracy in collective decision making. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**(1532), 2457–2463 (2003) [3](#)
7. Franks, N.R., Mallon, E.B., Bray, H.E., Hamilton, M.J., Mischler, T.C.: Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Animal Behaviour* **65**(1), 215 – 223 (2003) [2](#)
8. Franks, N.R., Stuttard, J.P., Doran, C., Esposito, J.C., Master, M.C., Sendova-Franks, A.B., Masuda, N., Britton, N.F.: How ants use quorum sensing to estimate the average quality of a fluctuating resource. *Scientific Reports* **5**(1), 11890 (2015) [18](#)
9. Franks, N., Richardson, T., Stroeymeyt, N., Kirby, R., Amos, W., Hogan, P., Marshall, J., Schlegel, T.: Speed-cohesion trade-offs in collective decision making in ants and the concept of precision in animal behaviour. *Animal Behaviour* **85**(6), 1233 – 1244 (2013) [3](#)
10. Gordon, D.M.: The ecology of collective behavior in ants. *Annual Review of Entomology* **64**(1), 35–50 (2019), PMID: 30256667 [2](#)
11. Hajek, B.: *Random Processes for Engineers*. Cambridge University Press (2015) [8](#), [15](#), [21](#), [22](#), [24](#)
12. Healey, C.I.M., Pratt, S.C.: The effect of prior experience on nest site evaluation by the ant *temnothorax curvispinosus*. *Animal Behaviour* **76**, 893–899 (2008) [2](#)
13. Hoeffding, W.: Probability inequalities for sums of bounded random variables. *Journal of the American Statistical Association* **58**(301), 13–30 (1963) [9](#), [21](#), [23](#)
14. Johnstone, R.A., Dall, S.R.X., Franks, N.R., Pratt, S.C., Mallon, E.B., Britton, N.F., Sumpter, D.J.T.: Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **357**(1427), 1567–1583 (2002) [2](#), [3](#)

15. Mallon, E., Pratt, S., Franks, N.: Individual and collective decision-making during nest site selection by the ant *leptothorax albipennis*. *Behavioral Ecology and Sociobiology* **50**(4), 352 – 359 (2001) [2](#), [6](#)
16. Marshall, J.A.R., Bogacz, R., Dornhaus, A., Planqué, R., Kovacs, T., Franks, N.R.: On optimal decision-making in brains and social insect colonies. *Journal of The Royal Society Interface* **6**(40), 1065–1074 (2009) [3](#)
17. Marshall, J.A., Dornhaus, A., Franks, N.R., Kovacs, T.: Noise, cost and speed-accuracy trade-offs: decision-making in a decentralized system. *Journal of The Royal Society Interface* **3**(7), 243–254 (2006) [3](#)
18. McGlynn, T.P.: The ecology of nest movement in social insects. *Annual Review of Entomology* **57**(1), 291–308 (2012), pMID: 21910641 [1](#)
19. Moglich, M.H.J.: Social organization of nest emigration in *leptothorax* (hym., form.) (1978) [2](#)
20. Planqué, R., Dornhaus, A., Franks, N.R., Kovacs, T., Marshall, J.A.R.: Weighting waiting in collective decision-making. *Behavioral Ecology and Sociobiology* **61**(3), 347–356 (2007) [3](#)
21. Pratt, S.C.: Behavioral mechanisms of collective nest-site choice by the ant *temnothorax curvispinosus*. *Insectes Sociaux* **52**(4), 383–392 (2005) [6](#)
22. Pratt, S., Mallon, E., Sumpter, D., et al.: Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *leptothorax albipennis*. *Behavioral Ecology and Sociobiology* **52**(2), 117–127 (2002) [2](#), [18](#)
23. Pratt, S.C.: Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behavioral Ecology* **16**(2), 488–496 (01 2005) [2](#), [3](#)
24. Pratt, S.C., Sumpter, D.J.T.: A tunable algorithm for collective decision-making. *Proceedings of the National Academy of Sciences* **103**(43), 15906–15910 (2006) [3](#), [6](#)
25. Pratt, S.C., Sumpter, D.J., Mallon, E.B., Franks, N.R.: An agent-based model of collective nest choice by the ant *temnothorax albipennis*. *Animal Behaviour* **70**(5), 1023 – 1036 (2005) [2](#), [6](#)
26. Richardson, T.O., Sleeman, P.A., Mcnamara, J.M., Houston, A.I., Franks, N.R.: Teaching with evaluation in ants. *Current Biology* **17**(17), 1520–1526 (Sep 2007) [2](#)
27. Robinson, E.J.H., Franks, N.R., Ellis, S., Okuda, S., Marshall, J.A.R.: A simple threshold rule is sufficient to explain sophisticated collective decision-making. *PLOS ONE* **6**(5), 1–11 (05 2011) [6](#)
28. Robinson, E.J., Smith, F.D., Sullivan, K.M., Franks, N.R.: Do ants make direct comparisons? *Proceedings of the Royal Society B: Biological Sciences* **276**(1667), 2635–2641 (2009) [6](#)
29. Sasaki, T., Colling, B., Sonnenschein, A., Boggess, M.M., Pratt, S.C.: Flexibility of collective decision making during house hunting in *temnothorax* ants. *Behavioral Ecology and Sociobiology* **69**(5), 707–714 (2015) [2](#), [3](#)
30. Stroeymeyt, N., Giurfa, M., Franks, N.R.: Improving decision speed, accuracy and group cohesion through early information gathering in house-hunting ants. *PLOS ONE* **5**(9), 1–10 (09 2010) [3](#)
31. Sumpter, D.J., Pratt, S.C.: Quorum responses and consensus decision making. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**(1518), 743–753 (2009) [3](#)
32. Visscher, P.K.: Group decision making in nest-site selection among social insects. *Annual Review of Entomology* **52**(1), 255–275 (2007), pMID: 16968203 [1](#)

A Proofs for Section 4

Theorem 3. (*Hoeffding's inequality, Theorem 2 in [13]*) If X_1, X_2, \dots, X_N are independent random variables with $a_i \leq X_i \leq b_i$ for $i = 1, \dots, n$, then for $D \geq 0$,

$$\mathbb{P} \left\{ \frac{1}{N} \sum_{i=1}^N (X_i - \mathbb{E}[X_i]) \geq D \right\} \leq \exp \left(\frac{-2N^2 D^2}{\sum_{i=1}^N (b_i - a_i)^2} \right).$$

Definition 2. (*Dobrushin's coefficient of ergocity, Page 181 in [11]*) Dobrushin's coefficient of ergocity $R(H)$ of a transition probability matrix H is

$$R(H) = \min_{i,k} \sum_j h_{ij} \wedge h_{kj},$$

where $a \wedge b = \min(a, b)$.

Proposition 3. For any round $t \geq 1$ and ant a_i , it holds that

$$\mathbb{P} \{T_i^1 > t\} < (1 - 2\alpha)^t = \beta^t,$$

where $\beta = 1 - 2\alpha$.

Proof. Let F^t represent the event that a_i is in state n_0 and does not transition out of n_0 during round t . That this could happen only if a_i has not jumped out of n_0 during any round previous to t as well. In turn, this requires that every coin toss that a_i has done

Further, F^t is influenced by the set of events $\{F^l\}$ for all $l \leq t-1$ only through F^{t-1} . Thus we have the following:

$$\begin{aligned} & \mathbb{P} \{F^t \mid F^{t-1} \wedge F^{t-2} \wedge \dots \wedge F^0\} \\ &= \mathbb{P} \{F^t \mid F^{t-1}\} \mathbb{P} \{F^{t-1} \mid F^{t-2}\} \mathbb{P} \{F^{t-2} \mid F^{t-3}\} \dots \mathbb{P} \{F^2 \mid F^1\} \mathbb{P} \{F^1\} \end{aligned}$$

For any given round $t \geq 2$, conditioned on F^{t-1} is true, the probability of any ant a_i still *not* transitioning out of n_0 during round t is $1 - 2\alpha(1 - \tau_1(t) - \tau_2(t)) - \tau_1(t) - \tau_2(t) < 1 - 2\alpha$. Furthermore, $\mathbb{P} \{F^1\} = 1 - 2\alpha$ since there are no ants leading tandem runs yet and $\tau_1(1) = \tau_2(1) = 0$.

Therefore,

$$\begin{aligned} \mathbb{P} \{T_i^1 > t\} &= \mathbb{P} \{F^t \mid F^{t-1} \wedge F^{t-2} \wedge \dots \wedge F^0\} \\ &= \mathbb{P} \{F^t \mid F^{t-1}\} \mathbb{P} \{F^{t-1} \mid F^{t-2}\} \mathbb{P} \{F^{t-2} \mid F^{t-3}\} \dots \mathbb{P} \{F^2 \mid F^1\} \mathbb{P} \{F^1\} \\ &= \mathbb{P} \{F^1\} \prod_{l=2}^t \mathbb{P} \{F^l \mid F^{l-1}\} \\ &= \prod_{l=2}^t \mathbb{P} \{F^l \mid F^{l-1}\} (1 - 2\alpha) \\ &< (1 - 2\alpha)^{t-1} (1 - 2\alpha) \\ &= (1 - 2\alpha)^t. \end{aligned}$$

Proposition 4. *Let T_i^1 be defined as in Definition 1. With probability 1, ant a_i transitions out of the state n_0 in finite time, i.e.*

$$\mathbb{P}\{T_i^1 < \infty\} = 1.$$

Proof. By definition, we know that $\{T_i^1 < \infty\} = \cup_{t=1}^{\infty} \{T_i^1 \leq t\}$. Thus, it holds that

$$\{T_i^1 = \infty\} = \{T_i^1 < \infty\}^c = (\cup_{t=1}^{\infty} \{T_i^1 \leq t\})^c = \cap_{t=1}^{\infty} \{T_i^1 > t\}.$$

It is easy to see that $\{T_i^1 > 1\} \supset \{T_i^1 > 2\} \supset \dots \supset \{T_i^1 > t\} \supset \{T_i^1 > t+1\} \supset \dots$. By continuity of probability [11, Lemma 1.1], we know that

$$\lim_{t \rightarrow \infty} \mathbb{P}\{T_i^1 > t\} = \mathbb{P}\{\cap_{t=1}^{\infty} \{T_i^1 > t\}\}.$$

In addition, from Proposition 3, we have

$$\mathbb{P}\{T_i^1 > t\} \leq (1 - 2\alpha)^t.$$

Therefore, we have that

$$\{T_i^1 = \infty\} = \mathbb{P}\{\cap_{t=1}^{\infty} \{T_i^1 > t\}\} = \lim_t \mathbb{P}\{T_i^1 > t\} \leq \lim_t (1 - 2\alpha)^t = 0,$$

proving the proposition.

Proof (Proof of Proposition 2). Notably the N indicator random variables are not independent. Hence, we prove this proposition via coupling. For each ant a_i , we introduce an auxiliary random variable \hat{T}_i^1 whose value is determined by a sequence of independent coin tosses one for each round. Each state transition of ant a_i during a round t is coupled with a coin toss as follows. The coin toss happens at the end of a round t . For any of the cases below, if the coin toss shows “HEAD”, set $\hat{T}_i^1 = t$.

- If ant a_i is not in n_0 at the beginning of t and $\hat{T}_i^1 > t - 1$, then toss a biased coin whose “HEAD” probability is 2α .
- If ant a_i is in n_0 at the beginning of round t and gets recruited during round t , then toss a biased coin whose “HEAD” probability is 2α .
- Otherwise, a.k.a. if ant a_i is in n_0 at the beginning of round t and does not get recruited during round t , the conditional probability of ant a_i leaving n_0 through independent discovery is 2α during round t . If ant a_i spontaneously leaves n_0 , toss a biased coin whose “HEAD” probability is 1; otherwise, toss a biased coin whose “HEAD” probability is 0.

Since initially all ants stay at home nest n_0 , under the above construction, it holds that $\hat{T}_i^1 \geq T_i^1$. Therefore, if $T_i^1 > t$, then $\hat{T}_i^1 > t$.

Summing up the cases listed above, for each a_i and each round t , if a_i has not transitioned out of n_0 by the end of round $t - 1$, the probability of her coin toss showing a head is thus 2α , i.e. ,

$$\mathbb{P}\{\hat{T}_i^1 = t \mid \hat{T}_i^1 \geq t\} = \begin{cases} 1, & \text{with probability } 2\alpha, \\ 0, & \text{otherwise.} \end{cases}$$

Moreover, let $E_{i,t} \triangleq \mathbb{1}\{\hat{T}_i^1 = t \mid \hat{T}_i^1 \geq t\}$. From the above construction, we know that for fixed a_i , $\{E_{i,t}\}_{t=0}^\infty$ are independent. Also, $\{E_{i,t}\}_{t=0}^\infty$ are *i.i.d.* across all ants.

We further define N independent random indicator variables $\mathbb{1}\{\hat{T}_i^1 > t\}$ for any t :

$$\begin{aligned} \hat{T}_i^1 > t &= \hat{T}_i^1 > t \mid \hat{T}_i^1 \geq t-1 \\ &= \neg(\hat{T}_i^1 = t-1 \mid \hat{T}_i^1 \geq t-1) \\ &= \neg E_{i,t-1}. \end{aligned}$$

Hence, for any t , the variables $\mathbb{1}\{\hat{T}_i^1 > t\}$ for each a_i are independent, each taking values in $\{0, 1\}$ and taking value 1 with probability $1 - 2\alpha$.

Since $\mathbb{1}\{T_i^1 > t\} = 1$ implies $\mathbb{1}\{\hat{T}_i^1 > t\} = 1$, it holds that

$$\sum_{i=1}^N \mathbb{1}\{T_i^1 > t\} \leq \sum_{i=1}^N \mathbb{1}\{\hat{T}_i^1 > t\}.$$

Combined with Hoeffding's inequality [13] (also Appendix A), we are ready to prove the proposition statement.

$$\begin{aligned} &\mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{T_i^1 > t\} < N((1-2\alpha)^t + d) = N(\beta^t + d)\right\} \\ &\geq \mathbb{P}\left\{\sum_{i=1}^N \mathbb{1}\{\hat{T}_i^1 > t\} < N(\beta^t + d)\right\} \\ &> 1 - \exp(-2Nd^2) \end{aligned}$$

Corollary 3. *With probability 1, all ants jump out of n_0 in finite time, i.e.,*

$$\mathbb{P}\left\{\max_{i \in [N]} T_i^1 < \infty\right\} = 1.$$

Proof.

$$\mathbb{P}\left\{\left\{\max_{i \in [N]} T_i^1 < \infty\right\}^c\right\} = \mathbb{P}\left\{\exists i \in [N] \text{ such that } T_i^1 = \infty\right\} = \sum_{i=1}^N \mathbb{P}\{T_i^1 = \infty\} = N \times 0 = 0.$$

Corollary 4 follows immediately from Corollary 3 and Proposition 1.

Corollary 4. *For any $t \geq \max_{i \in [N]} T_i^1 + 1$, the state transition $\mathbf{s}_i(t) \rightarrow \mathbf{s}_i(t+1)$ is independent of other ants. Moreover, for all $t \geq \max_{i \in [N]} T_i^1$,*

$$\mathbb{P}\{\exists i \in [N] \text{ such that } \mathbf{s}_i(t) = n_0\} = 0.$$

Proof (Proof of Corollary 1). For any given $\epsilon \in (0, 1)$, we can set $d = \frac{\epsilon}{2}$ and apply Proposition 2 and thus prove the statement.

Proof (Proof of Proposition 1). For ant a_i , at the beginning of round $T_i^1 + 1$, her state is either n_1 or n_2 . As can be seen from the state transition probabilities for each ant, once ant a_i jumps out of n_0 , i.e. at any time $t > T_i^1$, she can never return to n_0 according to Eq.(6)-(9).

Therefore, after T_i^1 , a_i 's state transition is independent of other ants, that is, the transition probabilities in Eq.(6)-(9) are not affected by the states of other ants.

Proof (Proof of Lemma 1). From Proposition 1 and Eq. 8, we know that for any $t \geq 1$, the state transitions of the ants in $Q(t-1)$ are independent of other ants. Hence, for any ant $a_i \in Q(t)$, her state transitions are governed by the transition matrix H which is defined in (7). From Proposition 4, we know that $\lim_{t \rightarrow \infty} Q(t) = \{1, \dots, N\}$ with probability 1. Thus, the stationary distribution of the colony state \mathbf{s} is well-defined and is unique. Denote this distribution by π . Note that π is a joint distribution of the states $\mathbf{s}_1, \dots, \mathbf{s}_N$ of all ants with π_i as the marginal distribution of π on the state of ant a_i . By symmetry, it holds that $\pi_i = \pi_j$ for any $i \neq j$. Solving the equation system $\pi_i = \pi_i H$, we get

$$\pi_i = \frac{1}{2 - u_1 - u_2} [1 - u_2, 1 - u_1].$$

Proof (Proof of Lemma 2). First note that at the beginning of round T_i^1 , the probability distribution of a_i 's state is such that the probability of state $s_i(T_i^1)$ (either nest n_1 or n_2) is 1 and of the new nest state she is not at is 0. By Proposition 1 we know that after T_i^1 , the dynamics of \mathbf{s}_i is Markovian. Hence we know that $\pi_{i, T_i^1 + \ell} = \pi_{i, T_i^1} H^\ell$.

It follows from [11, Proposition 6.5] that $\|\pi_{i, T_i^1} H^\ell - \pi^*\|_1 \leq 2(1 - R(H))^\ell$, proving the lemma.