

Nest-Level Phase Transition Drives Synchronized Activity Bursts in Ant Colonies

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Many natural complex systems exhibit synchronization, characterized by temporal coherence among the dynamics of their units. In ant colonies, synchronization manifests through activity bursts: sudden, sharp spikes of motion by a significant portion of workers throughout the nest, followed by durations of quiescence. These activity bursts were discovered three decades ago and studied since then; yet, the mechanisms that lead to their emergence remain elusive. Here, we present a model of ant activity that integrates both the motion of individuals within the nest and the transitions between behavioral states. By balancing microscopic behaviors in the model, we identify a nest-level phase transition from unsynchronized to synchronized activity and draw several connections between model predictions and empirical observations in the literature. Our analysis begets two key insights: (i) activity bursts emerge as a balance between the responsiveness of the colony to the first ant that activates and the ability of the colony to completely deactivate before the onset of the next burst, and (ii) the timescale of the motion of individuals through the nest is faster than that of the burst, suggesting that ants operate in a high-speed interaction regime where new behaviors are near-instantaneously transferred through the nest. We relate these findings to the broader literature on synchronization in complex systems, highlighting the need for periods of quiescence followed by the rapid communication of a new behavior through a population of connected units.

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I. INTRODUCTION

Since the observation of the “sympathy” of pendulum clocks by Huygens in the 17th century, synchronization, or the temporal coherence of individual dynamics in a collective, has remained at the forefront of physical and biological research [1–3]. Whether it be the synchronized bursting of neurons in the brain [4,5], the coherence of reacting chemical oscillators [6,7], or the coordinated flashing of fireflies [3,8,9], synchrony in complex systems emerges in almost every aspect of science. This prevalence, however, does not mean that a system capable of synchrony will, in fact, synchronize. In epidemiology, for instance, a disease can become endemic and exhibit periodic outbreaks across location and populations (synchronization) [10,11], rather than gradually decline after its initial peak [12,13]. This dichotomy

raises an important theoretical question: What characteristics of a complex system determine whether or not it synchronizes?

The activity patterns of ant colonies offer an ideal, and perhaps surprising, testbed to answer this question. Acorn ants, such as *Leptothorax acervorem* [14–16], *Temnothorax allardycei* [17,18], *T. rugatalus* [19], and *T. rudis* [20], use physical and social interactions to synchronize their activity in short-term periodic bursts where most of the colony move through the nest at the same time. Discovered almost simultaneously by Franks *et al.* [14] and Cole [17] three decades ago, the emergence of activity bursts has been hypothesized to assist the nest in improving spatial accessibility [21], and mitigating the spread of panic [22]. However, a wide range of species, including *Formica rufa* [23], *Diacamma* sp. [24], and *Atta colombica* [25], among others [26], exhibit diel foraging patterns, which are unlikely to support the emergence of bursts during peak foraging hours [16]. Using ants as a model for collective rhythmicity, we aim to shed light on coordinated complex systems and to more generally identify the mechanisms that promote or inhibit bursts of synchronized behavior in populations of interacting units.

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For complex systems to synchronize, information must be shared within the collective through the interactions among individuals [27]. In animal groups, such as schools of fish [28,29], flocks of birds [30,31], herds of sheep [32], and colonies of social insects [33–36], interactions unfold along multiple sensory pathways and along multiple temporal and physical scales. They are also instrumental for quick and robust responses to changing environmental conditions [37,38]. Alongside several other social systems [39], the form and function of interaction networks has been widely studied in ants. In colonies of harvester ants (*Pogonomyrmex californicus*), for example, the expected number of connections between conspecifics was found to grow with the size of the colony, allowing for faster information travel and an avenue for mitigating energy expenditure [36].

Early experiments and models of activity synchronization in ants established social interactions as the driver of rhythmic activity bursts [17,18]. The seminal model by Goss and Deneubourg [40,41] demonstrated that activity bursts in ants could result from active ants activating inactive ants, similar to contagious processes in epidemiological models [12] or autocatalytic chemical reactions [42]. Periods of activity are then followed by more or less fixed durations of rest, referred to as refractory periods. More recently, social deactivation—the inactivation of active workers by other active workers—was proposed as a mechanism for regulating the activity of ant colonies [36,43]. This social deactivation mechanism allows for active conspecifics to deactivate one another, incorporating an activity-driven negative social feedback term into the activity dynamics. In a previous work, we demonstrated that social deactivation does not eliminate the activity bursts and even allows the colony to vary its strength with growing colony size, providing a decentralized mechanism through which the colony is capable of mitigating overexertion [44].

While existing activity models provide insight into the emergence of the activity bursts, models that provide interpretations of activity bursts in a spatial context remain scarce. The recent formulation by Doering *et al.* [45] is likely the first to address this question through agent-based simulations that consider interactions between ants as they move through a virtual nest. The model, which also incorporates a refractorylike delay on the active state, predicts multirhythmic oscillatory behavior [45], similar to that measured in multiple species of ants [45,46]. Another recent spatial model of ant activity was put forward by Anderson *et al.* to explain waves of collective motion in dense populations of fire ants (*Solenopsis invicta*) [47,48]. However, the parameter constraints that support the onset of the synchronized activity were not explicitly addressed, and the relationship between the spread of activity and the motion of individuals through the nest was not detailed.

We thus set out with the following three objectives: (i) to establish a simple model of nest activity that accounts for the motion of, and interactions between, ants inspired by existing analysis of experimental data; (ii) to determine the key differences between colonies that exhibit activity rhythms and colonies that do not; and (iii) to quantify the onset of synchronization by balancing the relevant model characteristics, such as speed, cycle time, and the number of interactions. By considering the relationship between microscopic behaviors in the

model and the timing of the burst, we put forward closed-form estimates for the model conditions that incite synchrony within the colony. We compare estimates to simulations of the model, toward illustrating their validity across orders of magnitude. We conclude by demonstrating that reasonable parameter conditions place colonies of ants in a parametric regime where interactions occur significantly faster than the timescale of the burst, but that the social characteristics of the colony can easily position them near the transition threshold.

II. MATHEMATICAL MODEL

The presentation of the mathematical model is organized into three parts. In Sec. II A, we introduce the system geometry and how the ants move through space; in Sec. II B, we articulate interactions within the system and present an example of a unit of area coverage by the individuals; and in Sec. II C, we describe the probabilistic rules that govern activity transitions in ants. There are multiple parameters describing each of the model components, and their default values and empirical justifications can be found in Table I. Finally, we discuss a metric for quantifying synchronization over time in Sec. II D.

A. Movement

Based on extant literature [40,41], we assume that ants can be active, inactive, or refractory. Active ants are those moving in the nest chamber. Inactive and refractory ants are both immobile, but the former is capable of being activated while the latter is in a state of rest and cannot transition to activity. Inspired by results of Christensen *et al.* [50] and Hunt *et al.* [49] on *T. albipennis* ants, we characterize the movement of active ants (in a colony of size N) in a two-dimensional, periodic, square domain by stop-and-sprint-like rules of motion.

For each active ant, a movement bout is characterized by a fixed duration Ξ (min) and an orientation θ (rad). We choose the expected value of the movement bout, $\langle \Xi \rangle$, as the characteristic timescale of the model so that each unit in time represents, on average, a single bout duration. Thus, we use nondimensional variable $\xi = \Xi / \langle \Xi \rangle$ with expected value $\langle \xi \rangle = 1$. To nondimensionalize length to an ant species, we use the average distance from the center of mass of the body to the tip of the antenna—referred to as the effective antennal sector length, R —as the unit of spatial measure. This implies that the length of the domain, ℓ , is in units of the antennal sector length, and that results in space are discussed as a function of the extent over which ants can interact, making them more generalizable to an arbitrary range of ant sizes. We choose the nest density $\mu = N/\ell^2$ equal to one unless otherwise noted. For the *T. albipennis* ants measured by Hunt *et al.*, we set $\langle \Xi \rangle \approx 0.1$ min [49] and $R = 4$ mm [51].

The duration of a movement bout is treated as a continuous random variable pulled from a log-normal probability distribution, $\xi \sim \log N(1, 0.223)$, where we choose the coefficient of variation to be 0.5 [49] so that the variance is equal to 0.223 [53]. The speed over each movement bout maintains a power-law relationship with the duration of the event, $s(\xi) = s_0 \xi^\varphi$, where $\varphi \approx 0.25$ [49] is a positive exponent and s_0 is the nondimensional proportionality constant (speed constant). For increasing duration of the bout, the speed over the bout

TABLE I. Synoptic definition of parameters. The first column indicates the parameter domain; the second the name of parameter; the third the reference physical value from the literature and the unit of measure; the fourth the nondimensional value (range) adopted in the simulation; the fifth the nondimensional symbol used throughout the paper; the sixth the species being referenced; and the seventh the references from which the measurements are taken. Note that all nondimensional parameters except $(\mu, s_0, \rho, \beta, \tau)$ are fixed throughout the simulations; the reference values of these nondimensional parameters from data in the third column are $(\mu, s_0, \rho, \beta, \tau) = (1, 5.869, 0.02, 0.1, 750)$, and we explore ranges containing these values throughout the paper.

	Parameter	Nominal value	Simulation (nondimensional)	Symbol	Species	Ref.
System	Size Density	0.0625 mm ⁻²	100 [10 ⁻¹ , 10]	N μ		
Sec. II A: Movement	Expected movement duration	0.1 min	1	$\langle \xi \rangle$	<i>T. albipennis</i>	[49]
	Coefficient of variation	0.5	0.5		<i>T. albipennis</i>	[49,50]
	Rate of angular persistence	0.5 rad ⁻¹	0.5		<i>T. albipennis</i>	[49,50]
	Speed constant	417 mm min ^{-($\varphi+1$)}	[10 ⁻³ , 10]	s_0	<i>T. albipennis</i>	[49]
	Speed exponent	0.25	0.25	φ	<i>T. albipennis</i>	[49]
Sec. II B:	Radius	4 mm	1		<i>T. rudis</i>	[51]
Interaction network	Sensing range	$\pi/4$ rad	$\pi/4$	α	<i>L. humile</i>	[52]
Sec. II C: Activity transition rules	Spontaneous activation rate	0.002 min ⁻¹	0.0002	η		[40,41]
	Spontaneous deactivation rate	0.1 min ⁻¹	[10 ⁻⁴ , 1]	ρ	<i>T. rudis</i>	[44]
	Social activation rate	1 min ⁻¹	[10 ⁻² , 1]	β	<i>T. rudis</i>	[44]
	Social deactivation rate	0.1 min ⁻¹	0.01	γ	<i>T. rudis</i>	[44]
	Refractory delay	75 min	[500,1000]	τ	<i>T. rudis</i>	[44]

also increases, suggesting that ants that move for longer are covering more distance per unit time than if they are to draw more, shorter bout durations. We note two features of our choice for a single power law to represent the bout-speed relationship: (i) for longer bout durations, ants do not follow the predicted trend due to obvious physical limitations [49], and (ii) at small bout durations, measured ants move more slowly than the relationship predicts, likely due to acceleration limits in individual ants [49]. The first deviation occurs when the bout duration exceeds approximately $\xi > 16$ [49], which has probability $P(\xi > 16) < 10^{-15}$. The second occurs when $\xi < 0.25$ [49], with probability $P(\xi < 0.25) < 10^{-15}$. It is thus reasonable to conclude that neither of these outlier events will affect the overall activity dynamics.

At the start of a movement bout, t_0 , an active ant changes its direction $\theta \in [-\pi, \pi]$ using an adjustment pulled from a truncated Laplace distribution, centered at the origin, $\delta\theta \sim \text{TruncLap}(0.5; [-\pi, \pi])$, where 0.5 [49] is a nondimensional rate of angular persistence and $[-\pi, \pi]$ is the truncated range [54]. The heading update at t_0 is represented by the jump discontinuity,

$$\llbracket \theta(t_0) \rrbracket := \theta(t_0^+) - \theta(t_0^-) = \delta\theta. \quad (1)$$

Upon changing its orientation, the active ant moves uniformly along a straight line at a constant speed. We discretize the motion in time, using a resolution given by the time step δt , so that

$$\vec{x}(t + \delta t) = \vec{x}(t) + \vec{v}(t_0^+) \delta t, \quad (2)$$

where $\vec{x} \in \mathbb{R}^2$ is the position, $\vec{v}(t_0^+)$ is the velocity of magnitude s and orientation $\theta(t_0^+)$ in Eq. (1), and time t is updated

until reaching the movement bout duration ξ . We take the time step of the simulation to be $\delta t = 0.01$. This choice is used to mitigate small truncation errors when ξ is not an integer multiple of δt . For each result, we hold the values reported in the default parameter set (listed in Table I with the relevant citations) constant, unless otherwise noted.

B. Interaction network

Informed by biological constraints, we implement a sensing area for each ant that is parametrized by the effective antennal sector length, R , and angle, α . Having chosen the average antennal sector length as the characteristic length scale, the nondimensional interaction radius is one. Compelling arguments have been made for the range of α , suggesting that the angular range of the antennae can have an impact on the stability of foraging trails. Experiments conducted by Perna *et al.* [54] on Argentine ants (*Linepithema humile*) show that adjustments in the heading due to lateral imbalances in the pheromone concentration typically fell in the range $\pm\pi/4$. This is further supported by Amorim *et al.* [52], who mathematically proved that the angular range of the sensing area must be $\alpha < \pi/2$ for individuals to reliably follow pheromone trails. With these results in mind, we choose $\alpha = \pi/4$ as a biologically reasonable value for the “typical” sensing angle.

Two ants, i and j , are considered physically connected if (i) the distance between them, $d_{i,j}(t) = \|\vec{x}_i(t) - \vec{x}_j(t)\|$, is less than 1, where $\|\cdot\|$ denotes the Euclidean norm, and (ii) the angular sector of the sensing area of ant i contains the position of ant j , or vice versa [Fig. 1(a)]. The check for condition (ii)

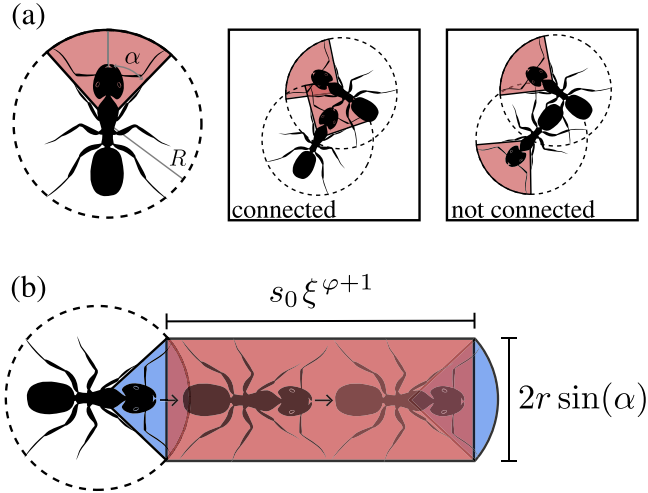


FIG. 1. Parameters governing ant interactions in the model. (a) The sensing area and an example interaction between two ants. (b) Over a bout of movement, an individual is capable of interacting with other ants in the domain spanned by its duration-specific area coverage (red). We neglect the edge of the area coverage (blue), assuming it is small in comparison to the movement bout.

is

$$\arctan \left(\frac{x_i^{(2)}(t) - x_j^{(2)}(t)}{x_i^{(1)}(t) - x_j^{(1)}(t)} \right) \in [\theta_i(t) - \alpha, \theta_i(t) + \alpha], \quad (3)$$

where superscripts (1) and (2) denote the components of the position vector in the Cartesian coordinate system, and all angular quantities are wrapped to the interval $[-\pi, \pi]$.

Over a movement bout, an active ant can interact with other ants in the span of its sensing area [Fig. 1(b)]. We depict the sensing area spread over a movement bout and estimate the bout-specific area coverage by taking the product between the span of the sensing area and the distance covered during the movement bout ($s_0 \xi^{\varphi+1}$):

$$A = 2s_0 \xi^{\varphi+1} \sin(\alpha). \quad (4)$$

An active ant interacts with any ant whose position falls in the span of A during the movement bout.

C. Activity transition rules

To transition between the active, inactive, and refractory states, we implement rules inspired by Goss and Deneubourg's autocatalytic model of activity [40] and its recent expansion by Porfiri *et al.* [43] and Napoli *et al.* [44] that includes the activity-driven social deactivation mechanism. For demonstration, we follow a focal ant as it cycles from the active state (a) to the refractory state (r), then to the inactive state (b), and finally back to the active state.

In each time step, we consider the ant to be connected with k active ants in the environment. Starting in the active state, the ant may transition to the refractory state by two processes: either (i) spontaneously, with a fixed, nondimensional rate ρ and scaled by the length of the time step to retrieve the probability $P(a \rightarrow r; \rho \delta t) = \rho \delta t$, or (ii) through interactions with other active ants, where each of k instantaneous

interactions is modeled as an independent Bernoulli trial with a nondimensional success rate γ , so that the probability of transitioning becomes $P(a \rightarrow r; \gamma \delta t, k) = 1 - (1 - \gamma \delta t)^k$. Being that processes (i) and (ii) are independent, the joint probability of transitioning becomes

$$P(a \rightarrow r) = 1 - (1 - \rho \delta t)(1 - \gamma \delta t)^k. \quad (5)$$

Once in the refractory state, the ant transitions to the inactive state only after a fixed period of nondimensional time, referred to as the refractory delay τ , and with probability one.

An inactive ant transitions back to the active state by one of the following two processes: (i) spontaneously, with nondimensional rate η and probability $P(b \rightarrow a; \eta \delta t) = \eta \delta t$, or (ii) through an interaction with k already active ants, with nondimensional rate β and probability $P(b \rightarrow a; \beta \delta t, k) = 1 - (1 - \beta \delta t)^k$. Similar to Eq. (5) we write the joint transition probability

$$P(b \rightarrow a) = 1 - (1 - \eta \delta t)(1 - \beta \delta t)^k. \quad (6)$$

We evaluate these rules at every time step and use the network constructed by the interactions discussed in Sec. II B.

Some parameters in the model—the spontaneous and social transition rates and the delay length—are difficult to infer from available behavioral data. This challenge primarily arises due to lack of detailed interaction data needed to calibrate social activation rates, and to the inability to distinguish ants in the inactive and refractory states, which are both immobile [43].

Estimates can be obtained using colony-level activity measurements. In previous work, we used activity time series reported by Doering *et al.* [20] to estimate $(\rho, \beta, \gamma, \tau)$ for colonies of *T. rudis* [44]. These estimates were computed by minimizing the difference between scaling relationships observed in the data and predictions of a mean-field model with analogous transition dynamics to those described above. This procedure yielded approximate values $\rho \approx 0.01$, $\beta \approx 0.1$, $\gamma \approx 0.01$, and $\tau \approx 750$ in nondimensional units [44].

To the best of our knowledge, the spontaneous activation rate, η , has not been quantitatively calibrated in the literature. Existing studies, however, suggest that burst dynamics arise only when spontaneous activation is very rare [40,41], consistent with observations that isolated ants activate far less frequently than ants within a group [14,18]. Consequently, η can be assumed to be small relative to the other transition parameters, leading us to set it to a nominal value of $\eta = 0.0002$, equal to that used in extant mean-field models of activity rhythms [40,55].

D. Phase coherence

Crucial to our analysis is the ability to differentiate between a time series with activity bursts and one without. In synchronization analysis, one typically considers an order parameter that quantifies the temporal alignment between units in the system [7,56]. For example, the Kuramoto model, a template model for such phenomena, comprises individual oscillators with a common oscillation frequency [57,58]. In this case, the synchronization of the system can be captured by comparing the difference in the angular coordinate between pairs. In the model presented here, the activity cycle of an ant

is expected to follow a natural rhythm. Yet, due to the stochastic process governing the transitions, an individual's activity cycle may significantly deviate from any expected duration, making it necessary to carefully define the phase-dependent order parameter.

We introduce phase coherence as a measure of phase locking of ant transitions on a global activity cycle. Let $\mathbb{A} = \{a, b, r\}$ be the set of possible states and $\vec{\psi}(t) \in \mathbb{A}^N$ be a snapshot at time t of the colony. At each time step, we define the level of activity in the system as $\mathcal{A}(t) = \frac{1}{N} \sum_{i=1}^N \mathbb{I}(\vec{\psi}_i(t) = a)$, where $\mathbb{I}$ is an indicator function, equal to one when the argument is true (ant i is active at time t) and zero otherwise. We use $\mathbb{X}_a$ to identify the discrete range of possible levels of activity. We assign to each ant a phase $\chi_i(t) \in [0, 2\pi)$, setting $\chi_i = 0$ at the moment the ant transitions into the active state. The phase then increases linearly until the next activation, with each interactivation interval normalized to 2π . This procedure yields a piecewise-linear phase variable whose first derivative is also piecewise constant.

Given the set of instantaneous phases, phase coherence is written as

$$\varsigma_\chi(t) = \left| \frac{1}{N} \sum_{i=1}^N e^{i\chi_i(t)} \right|, \quad (7)$$

where i is the imaginary unit. Phase coherence takes values in $[0, 1]$, with $\varsigma_\chi = 1$ corresponding to complete synchronization and $\varsigma_\chi = 0$ to incoherence (phases uniformly distributed for $N \rightarrow \infty$). While phase coherence quantifies phase locking in oscillator systems, it comes with two practical limitations. First, comparison of the degree of synchronization of systems of different sizes may be confounded by the dependence of phase coherence on the burst amplitude [44]. Second, in experimental data of colonies of ants, it is difficult to accurately label the activity states of individuals.

An alternative approach that overcomes these limitations is the use of recurrence maps [59], a popular method for transforming discrete time-series data into a network of connected nodes [60]. Recurrence maps allow one to leverage the broad field of network analysis to study underlying patterns in temporal phenomena [60, 61], and are built by connecting points in time when trajectories in the system are close in phase space (see Appendix A for mathematical details). Using this network of connections, one can compute the determinism, a metric that reflects how predictable the underlying time series is over long periods of time (Appendix A). High determinism in our case reflects either (i) a constant level of activity or (ii) periodic oscillations. Careful selection of the threshold used to build the recurrence map, however, allows us to dismiss the former as a reason for high determinism, as the metric will naturally decrease for phase-space trajectories stochastically varying around a mean value (Appendix A). In contrast with phase coherence, determinism (i) is agnostic to the shape of the bursts and (ii) mitigates the need for behavior data at the individual level.

III. RESULTS AND DISCUSSION

Our analysis is organized into three parts. In Sec. III A, we show that the model is capable of generating periodic

activity bursts under empirically grounded parameters and we present the first-mover mechanism. Then, in Sec. III B, we identify the speed constant, s_0 , as a key control parameter governing the emergence of activity bursts, and show parameter-dependent transitions from synchronized to unsynchronized activity under high-speed conditions. We conclude by deriving order-of-magnitude estimates of the phase transition using arguments driven by the first-mover mechanism in Sec. III C.

A. Burst synchronization and the first-mover mechanism

We note that the parameters describing motion and those describing the transition between activity states come from two different species of ants: *T. albipennis* [49] and *T. rudis* [44]. We justify this parametrization choice using two arguments. First, the workers of both species have strikingly similar morphologies [62, 63], implying that their accessible speed range and motion are likely comparable [51]. Second, activity rhythms have been measured in a broad range of *Temnothorax* ant colonies [20]. While rhythms have not been measured explicitly in *T. albipennis* colonies, Doering *et al.* [20] demonstrated that collective rhythmicity is an evolutionary trait which can be traced across both the *Temnothorax* and *Leptothorax* genera, suggesting that the two species may also behave similarly from an activity perspective.

We run simulations for $N \in \{100, 1000\}$ ants using the nondimensional form of the dimensional values given in Table I (third column). Simulation results indicate that the model is successful in reproducing short-term period bursts of *T. rudis* [20]; we simulated 10^4 units of time but only plot (and take measurements over) the last 5000 units to neglect the initial transient response of the system. The peaks of the bursts have a range of approximately $[0.25, 0.75]$ and occur with a period of approximately 1000 units of time (approximately 100 min), in line with Ref. [20]. When $N = 1000$, the peak height diminishes to approximately 0.3 with noticeably less instances of dramatic variations in the amplitude.

To assess whether a homogeneous-mixing assumption is reasonable in the model, we compute the pairwise distances between ants across 100 independent realizations of an activity burst (samples taken $\Delta t = 5$ units of time apart). The probability density p of two ants i and j being a distance of d apart is unimodal with asymmetric tails [Fig. 2(b)]. The distribution increases linearly, $p(d) = (2\pi/\ell^2)d$, up to a threshold of $\ell/2$, after which it decreases rapidly to zero at the bounds of the distance distribution $\ell/\sqrt{2}$ (the maximum distance on a torus of length ℓ). This nonmonotonic pattern arises from the square geometry of the domain, whereby distances can be partitioned between ants within the maximal inscribed circle (of diameter $\ell/2$) and ants located outside such a circle (opposite corners) whose distances exceed $\ell/2$. The computed distribution is consistent with that of homogeneous mixing, and holds for variations in the density (see Appendix B for details).

To probe the mechanism underlying burst emergence, we show the activity dynamics over a representative burst [Fig. 3(a)] and emphasize that a single ant is capable of sparking the spread of activity through the nest [Figs. 3(b) and 3(c)]. At the peak of the activity burst [Fig. 3(d)], a large proportion

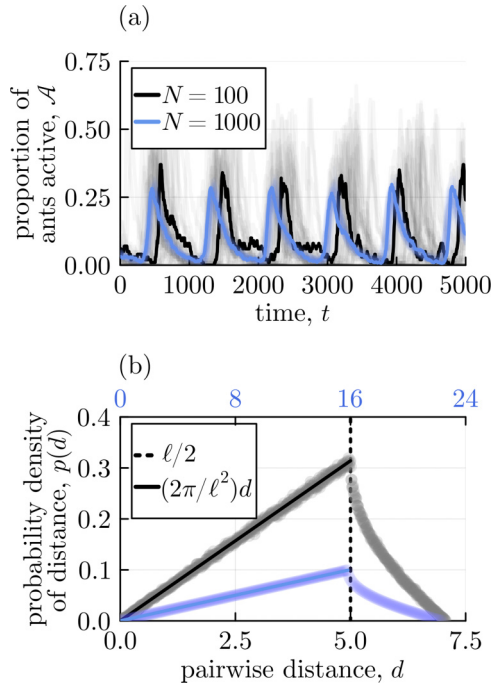


FIG. 2. The model exhibits synchronized bursts of activity. Simulations are performed on colonies of size $N \in \{100, 1000\}$ (black and blue, respectively) ants for 10^4 time units, focusing on the last 5000 steps for analysis. All parameter values are specified in Table I (fourth column) except those given by ranges which we set to $(\mu, s_0, \rho, \beta, \tau) = (1, 5.869, 0.01, 0.1, 750)$. (a) The steady-state activity patterns replicate rhythmic bursts observed in real colonies of *T. rudis* [20]. A single replicate (of 50) is highlighted by a single, solid curve in both system sizes. We note that the smaller system exhibits significantly more variation in the amplitude of the bursts, reaching levels of activity as high as approximately 0.7. (b) We find that the probability density of the pairwise distance between ants supports a homogeneous mixing assumption in both system sizes. The probability density grows linearly with slope $2\pi/\ell^2$ toward $\ell/2$ (solid line), before a sharp decrease in probability approaching the maximum distance between any two pairs of ants, $\ell/\sqrt{2}$.

of the nest has activated before the activity dynamics reset to an immobile state [Fig. 3(e)]. We refer to the first ant activated in a burst as a “first mover” and find that the ability for an arbitrary ant to excite activity in the nest, similar to the cascade expected from falling dominoes, is indicative of the emergence of the burst.

To study the cascading of activation in the colony, we construct an activation graph [Fig. 4(a)]. In the activation graph, an outgoing connection from ant i to j is formed when j activates due to an interaction with active ant i ; note that the assembly of such a network relies on the possibility to separate spontaneous from social activation in the numerical simulations. For an arbitrary ant, its depth in the activation graph is characterized by the minimum number of edge traversals required to reach the ant from the root of the graph (the burst’s first mover). To gain statistical insight, we compute relevant statistics over 250 independent realizations [Figs. 4(b) and 4(c)]. Specifically, we plot the probability of a node residing at a given depth [Fig. 4(b)] and note two important features: (i) the likelihood of being a root node in

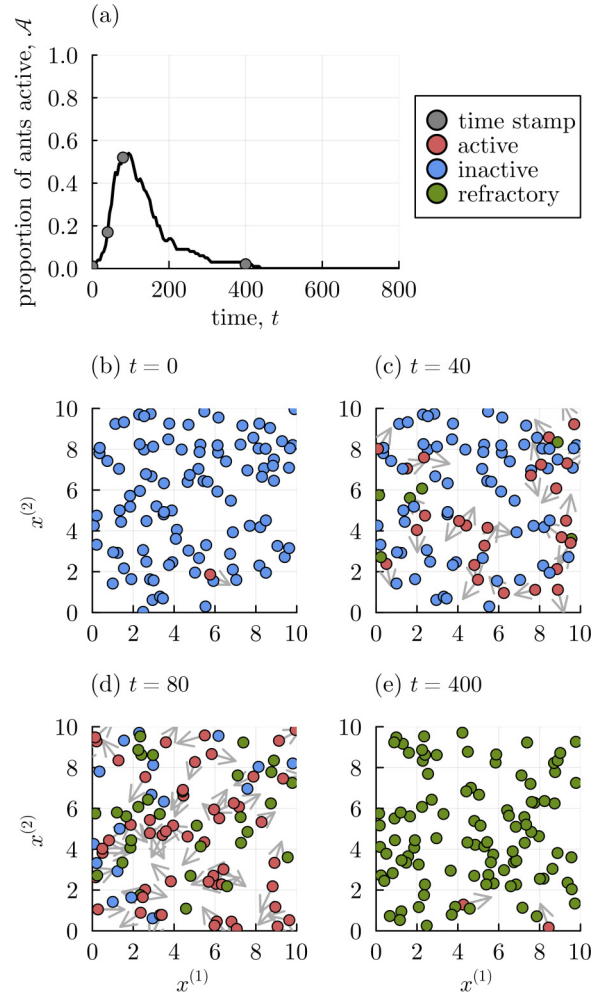


FIG. 3. A single ant is capable of exciting the entire nest. (a) The burst begins from (b) a single active ant, (c) who rapidly spreads activity through the rest of the nest. (d) Around the peak, the population becomes approximately evenly distributed between the three states. (e) Finally, the majority of the ant population ends in the refractory state, completing the activity cycle. A video depicting the entire burst window is shown in the Supplemental Material (Supplemental Video I [64]). To extract the burst, we simulate the model for 800 units past the end of the steady-state simulation shown in Fig. 2(a) for $N = 100$ ants and manually select steps that correspond to meaningful points in the dynamics.

the activation graph (no incoming connections) is a local minimum with a probability of approximately $1/N$, and (ii) the probability peaks around a depth of approximately five jumps from a first mover. The first result suggests that secondary roots (ants that activate spontaneously but occur later in time from the first mover) are extremely rare, with a probability of occurring $\ll 1/N$. The peak represents a measure of the depth at which the environment becomes saturated with activity, and the occurrence of later nodes becomes less likely as the spread of activity exhausts the population of ants. Additionally, we calculate the expected number of activations by an ant as a function of its depth in the activation graph [Fig. 4(c)]. A first mover activates on average the most ants in the environment, acting as a spark that excites the systemwide activity burst.

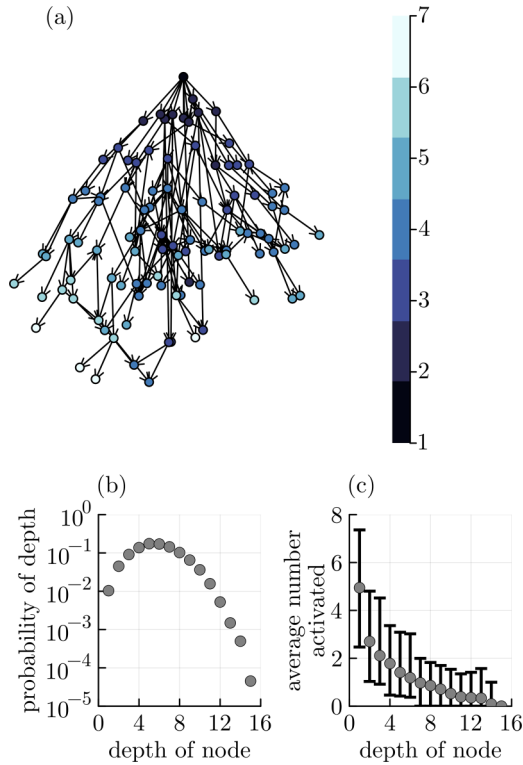


FIG. 4. Activation graph depiction of the cascade of activity through the nest. (a) The activation graph demonstrates the presence of a single first mover. The color of each ant represents the minimum number of edges between that ant and the first mover of the activation graph. (b) We compute the probability that an ant resides at a given depth on the activation graph. A first mover has a probability of approximately $1/N$, suggesting that a single, arbitrary ant begins each activity burst. (c) The average number of activations by each node as a function of the node's depth in the activation graph. To compute the activation graph, we simulate the model for 800 units beyond the steady-state replicates illustrated in Fig. 2(a) for $N = 100$ ants, keeping all parameters constant. This process is repeated for 50 replicates and the resulting set of activation graphs is used to compute statistics.

The significance of a single ant in shaping colony-level activity aligns with prior studies in acorn ants. A study by Boi *et al.* [16] on *L. acervorum* found that colonywide activity often originated in minute local regions of the nest, propagating outward isotropically. Interestingly, to model the activity waves, they partitioned the nest into two subpopulations—the brood pile group and the entrance group—and found that the entrance group exhibited disrupted activity bursts due to irregular perturbations by returning foragers, while the brood pile group maintained consistent burst patterns. This observation supports the idea that locally initiated activations can seed systemwide bursts, while “off-schedule” activations (returning foragers who enter the nest active) only serve to disrupt the burst. Though speculative, this connection motivates future experimental studies aimed at providing perturbations to the nest in an attempt to disturb or generate activity bursts.

B. Speed and the phase transition

Existing studies of complex systems [37,65] often discuss the concept of an effective temperature: a single parameter

that summarizes “the relative change in the number of microscopic states of a system with change in the internal energy” [66] and helps quantify energy dissipation toward equilibrium [66,67]. While the speed constant s_0 does not serve as a precise indicator of the temperature of the system, it does constitute a meaningful control variable through which one may parametrize the emergence of the activity bursts.

When $s_0 \rightarrow 0$ (low speed), ants do not change their position and the system behaves akin to the XY model, where each particle is restrained to the vertex of a lattice and given a spin (heading direction) that is uncorrelated to its neighbors [68]. When $s_0 \rightarrow \infty$ (high speed), the interactions between ants become increasingly uncorrelated with time, and the model behaves similarly to a homogeneous random mixture. This can be recognized by defining the persistence time, or the expected time during which ants stay connected to one another. Given that the interaction radius is one and the average speed is proportional to s_0 , the persistence time is estimated as $\lambda = s_0^{-1}$. As s_0 increases, the persistence time $\lambda \rightarrow 0$, each duration redrawing the contact set in the next measurement period.

1. Low speed

To demonstrate that s_0 is a meaningful control parameter, we test how the phase coherence varies with changes in the speed constant [66]. We run simulations for $N \in \{50, 100, 500, 1000\}$ ants using the parameters defined in Table I (fourth column), with the parameters given by ranges set to $(\mu, \rho, \beta, \tau) = (1, 0.01, 0.1, 750)$. The model is simulated for 10^5 units of time, with the latter 9×10^4 units of the time series used for analysis. This process is repeated for each speed constant in the range $s_0 \in [10^{-3}, 10]$ (17 points), and the resulting activity time series are used to compute the mean and standard deviation of the coherence (Fig. 5). We find that at a certain threshold in the speed constant, the model synchronizes for all subsequent values of s_0 , implying that when the ants move faster than a certain threshold, activity is more capable of propagating through the nest (Fig. 5). The synchronization threshold is largely invariant with respect to the size of the system, but becomes more consistent when increased by a factor of 10 (indicated by a smaller magnitude in the standard deviation). This is further validated by the determinism, which depicts the same transition point for variations in the speed constant (Appendix A).

Additionally, we compute the active state distribution, $P(\mathcal{A})$, which represents the discrete probability that the proportion of ants that are active in the colony is $\mathcal{A}$ and serves as an observable over the full state-space distribution, $P(\vec{\psi})$. Interestingly, even in the small N considered here, beyond the phase transition the decay of the distribution is reminiscent of Zipf’s law, $P(\mathcal{A}) \propto 1/r(\mathcal{A})$, where r reflects the ranked occurrence of $\mathcal{A}$ over time (inset to Fig. 5). In thermodynamics, the emergence of Zipf’s law is a landmark of systems of particles near a transition threshold, whereby the relationship between probability and rank is indicative of the increased prevalence of high-entropy states in the system and points toward a linear relationship between entropy and energy

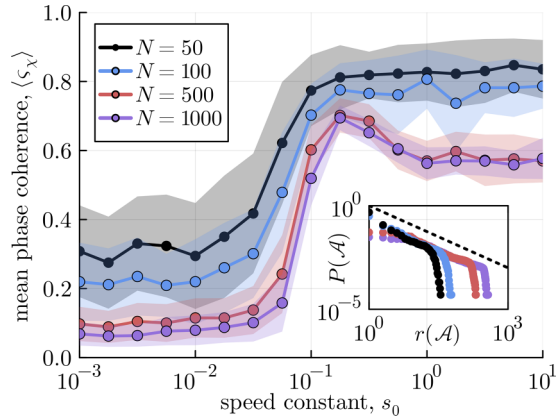


FIG. 5. The speed constant, s_0 , as a suitable control parameter in the model. Simulations are run for variations in speed $s_0 \in [10^{-3}, 10]$ (17 points) using the parameter set described in Table I with $(\mu, \rho, \beta, \tau) = (1, 0.01, 0.1, 750)$ and $N \in \{50, 100, 500, 1000\}$ ants. The model is simulated for 10^5 units of time, considering only the latter 9×10^4 units in our analysis. We plot the mean of the phase coherence (solid curve) and standard deviation (shaded region) as a function of the speed constant and identify a transition threshold, $s_0 \approx 0.06$, above which the model synchronizes for all subsequent values of s_0 and for both values of N . For each s_0 , we compute the discrete probability that the proportion of ants is $\mathcal{A}$ and find that beyond the transition threshold (inset, $s_0 = 0.1$), the distribution sorted by the rank of occurrence resembles Zipf's law (slope indicated by the dotted black line).

[69,70]. We note that validation of Zipf's law requires scoring the full state-space distribution, $P(\vec{\psi})$, which in our case entails measuring the frequency of 3^N unique microscopic states [71]. Our proxy, however, offers a meaningful observable over $\vec{\psi}$ for gauging the increased prevalence of high-activity states.

We now vary both the speed, s_0 , and the density, μ , in a simulation of $N = 100$ ants (Fig. 6). Simulations are run with $N = 100$ ants and $s_0 \in [10^{-3}, 10]$ (51 points), while varying density, $\mu \in [10^{-1}, 10]$ (51 points). With respect to the remaining parameters, we choose those given in Table I except for ρ , β , and τ , which we set to $(\rho, \beta, \tau) = (0.01, 0.1, 750)$. For each (s_0, μ) pair, we simulate the model for 10^5 units of time, with the last 9×10^4 units used for analysis. At high enough density, the interaction network becomes compact, so that bursts emerge even in the absence of motion. This is observed for $\mu \gtrsim 3$, where the model synchronizes for all measured values of speed, s_0 .

To the best of our knowledge, the relationship between population density and the emergence of activity bursts is still unknown, despite being central to other emergent behaviors (e.g., groups of locusts [72] and flying midges [31]). The closest quantification comes from experiments conducted by Anderson *et al.*, where extremely packed populations of fire ants exhibit measurable, slow-moving spatial waves above a certain threshold in the packing fraction [47,48]. Similarly, above $s_0 \approx 0.01$, the model is capable of synchronizing for smaller density, but relies heavily on the emergence of a compact network topology in the slow-speed regime, a result of the increased difficulty for ants to form persistent long-range connections in the nest.

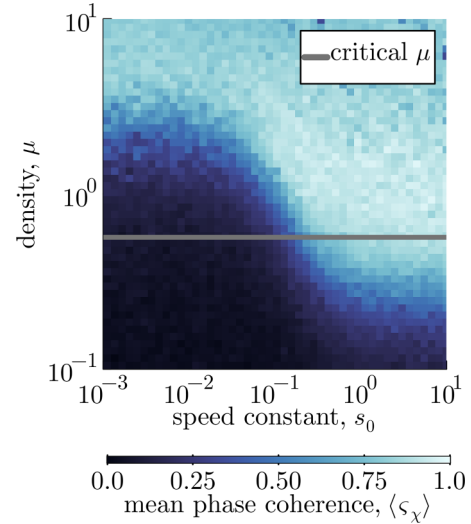


FIG. 6. Changes in the phase boundary for variations in the speed and density. The density is varied over $\mu \in [10^{-1}, 10]$ (51 points) for each $s_0 \in [10^{-3}, 10]$ (51 points) in a system of $N = 100$ ants. The remaining parameters, and the analysis of the activity time series, are otherwise synonymous with Fig. 5. When the density is high ($\mu \gtrsim 2.5$), the interaction network between conspecifics becomes compact and bursts emerge even in the absence of motion. Increasing speed likewise improves the spread of activity, allowing bursts to emerge for lower density, as predicted by balance [Eq. (10)].

2. High speed

Following similar procedures to those for Vicsek-type systems [73], we next focus on a high-speed regime. The validity of a high-speed assumption in ant colonies is supplemented by the magnitude of the proportionality constant calculated by Hunt *et al.* in species of *T. albipennis* ants [49]. In their experiments, the proportionality constant relating speed and movement duration was $\approx 417 \text{ mm min}^{-(\varphi+1)}$, corresponding to a nondimensional proportionality constant $s_0 \approx 5.869$. This speed constant creates a persistence time in the nest of approximately $\lambda = 0.170$, which is six times smaller than the timescale of the movement bout.

We run simulations for $N \in \{50, 100, 500, 1000\}$ ants and the nondimensional parameter values given in Table I (fourth column). With respect to the four parameters given by ranges in the table, we choose values corresponding to a high-speed regime, namely, $(\mu, s_0, \beta, \tau) = (1, 10, 0.1, 750)$, and for ρ we consider rates logarithmically spaced in $[10^{-4}, 1]$ (13 points). Changing the deactivation rate, the ants synchronize their activity around a singular value in ρ , identified by a sharp peak in the coherence computed over the time series [Fig. 7(a)]. The phase coherence peaks at $\rho \approx 0.033$ (dimensionally equivalent to 0.33 min^{-1}) with valleys of low coherence on either side. This trend is persistent across scales, whereby the coherence exhibits a peak in approximately the same position with a tenfold increase in the system size. The transition to synchronized activity is also demonstrated accurately by the determinism of the time series (see Appendix A).

To study the position of the peak for varying β , we logarithmically vary $\rho \in [10^{-4}, 1]$ (51 points) and $\beta \in [10^{-2}, 1]$

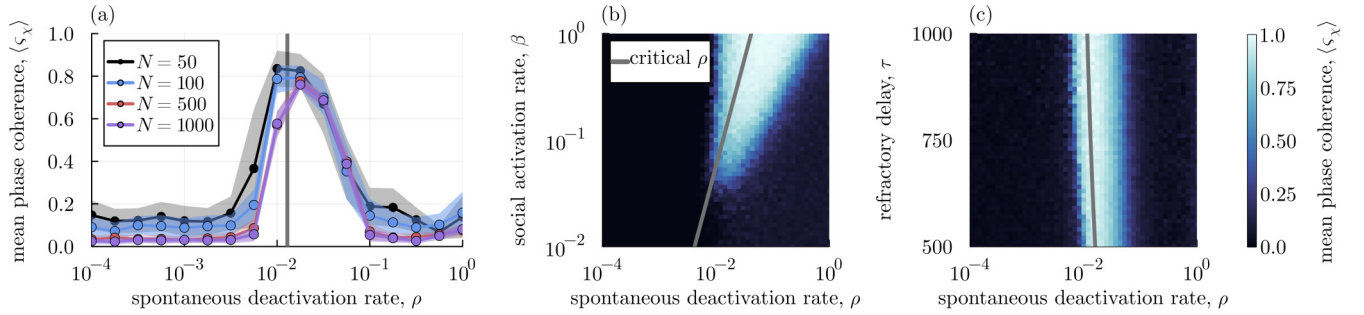


FIG. 7. Changes in the phase transition in the model's high-speed regime. (a) Simulations are run for $N \in \{50, 100, 500, 1000\}$ ants and parameters chosen from Table I with $(\mu, s_0, \beta, \tau) = (1, 10, 0.1, 750)$. The spontaneous deactivation rate is logarithmically varied, $\rho \in [10^{-4}, 1]$ (13 points). All simulations are run for 10^5 units of time, with the last 9×10^4 being used for analysis. We illustrate the mean phase coherence (solid curve) and standard deviation (shaded region) for the model in a high-speed regime. A peak in the coherence exists at $\rho \approx 0.033$ and is estimated well by Eq. (10) (gray vertical line). (b) The model is then simulated for $N = 100$ ants and $\rho \in [10^{-4}, 1]$ (51 points) while varying $\beta \in [10^{-2}, 1]$ (51 points). All remaining parameters are set to the values chosen in (a) for the same length of time. (c) Similarly, we vary the delay $\tau \in [500, 1000]$ (51 points) for the same range of ρ , with ten replicate simulations for each (ρ, τ) pair. The accuracy of the transition ρ from Eq. (10) is maintained across scales of β and τ , as shown by the gray curve. The blue shading denotes the magnitude of the phase coherence for each pair (ρ, β) and (ρ, τ) measured, with lighter shading representing higher coherence.

(51 points). The rest of the nondimensional parameter values are chosen as reported Table I (fourth column) and with $(\mu, s_0, \tau) = (1, 10, 750)$. The blue coloration represents the mean magnitude of $\langle \zeta_x \rangle$ in a simulation of length 10^5 , with the latter 9×10^4 units of time used for analysis [Fig. 7(b)]. For varying τ , we repeat this process under the same parameter conditions, but with $\beta = 0.1$ and for $\tau \in [500, 1000]$ (51 points). When $\beta \ll 1$, ants do not synchronize their activity for any measured value of ρ , owing to the low probability of spreading activity during social interactions. When β approaches the empirical value of 0.1, we identify a region of synchronized activity in ρ .

C. Predicting synchrony in the model

The nonmonotonic trend in the phase coherence (Fig. 7) suggests the existence of two competing mechanisms, the intersection of which creates the bursts. We hypothesize these mechanisms to be (i) the expected number of activations during the activity stint of a first mover, $\langle n_a \rangle$, and (ii) the ratio between the time spent active and the time spent “resting,” $\tilde{\tau}_a$ (which we refer to as the active-rest ratio). By equating the magnitudes of mechanisms (i) and (ii), we offer insight into the dependence of the phase transition on model parameters, which we subsequently compare to our numerical simulations.

First, we estimate $\langle n_a \rangle$. Being that the ants are homogeneously mixed, the expected number of ants a first mover interacts with, $\langle n \rangle$, is directly proportional to the area covered over their activity bout. We additionally infer that a first mover deactivates spontaneously, a result of the initial sparsity of active ants in the environment (Fig. 3). Under these considerations, the number of interactions is parametrized by (i) the expected duration-specific area coverage, $\langle A \rangle$, (ii) the expected number of movement durations drawn during the activity bout, $1/\rho$, and (iii) the persistence time, λ . In a nest with density μ , this yields $\langle n \rangle = \mu \langle A \rangle \lambda / (\rho \delta t)$, which increases as $\delta t \rightarrow 0$ to reflect increases in the measurement frequency with decreasing time step. To estimate the number of activations by a first mover, we simply divide $\langle n \rangle$ by the expected spacing

between activations in a series of measurements, $1/(\beta \delta t)$. This results in

$$\langle n_a \rangle \approx (\beta \delta t) \langle n \rangle = 2\mu \frac{\beta}{\rho} \sin(\alpha), \quad (8)$$

which is invariant to changes in s_0 and δt . We note that $\langle n_a \rangle$ reflects an upper bound on the number of activations, as the social deactivation rate γ practically caps the time spent in the active state. For $\gamma \ll 1$, however, we expect the contribution of γ to be negligible.

Second, we estimate the active-rest ratio $\tilde{\tau}_a$ from the time a focal ant spends in each of the activity states. An upper bound on the time spent in the active state is established by neglecting the influence of social deactivation, whereby we expect that each ant spends approximately $\tau_a = 1/\rho$ units of time active. Following the transition from the active state, each ant spends the same amount of time in the refractory state, allowing us to write $\tau_r = \tau$. For the time spent in the inactive state, we consider the minimum wait time before a first mover activates, which, in the presence of a burst, coalesces into a near-instantaneous wave of activations. Under this premise, $\tau_b = 1/(N\eta)$ units of time (see Appendix C for more details). Combining the expectation for the time spent in the active, inactive, and refractory states yields an upper bound on the active-rest ratio,

$$\tilde{\tau}_a \leq \frac{\tau_a}{\tau_b + \tau_r} = \frac{1}{\rho \left(\frac{1}{N\eta} + \tau \right)}. \quad (9)$$

We expect the active-rest ratio to be small, $\tilde{\tau}_a \ll 1$, to allow for the population of active ants to completely deactivate before the onset of the next activity burst, effectively resetting the activity dynamics.

Parametrized by the spontaneous deactivation rate, ρ , Eqs. (8) and (9) both change proportionally to $1/\rho$. For activity bursts to emerge, $\langle n_a \rangle$ should be large (promoting the spread of activity) and $\tilde{\tau}_a$ should be small (allowing the activity dynamics to reset). We thus balance the upper bound on $\tilde{\tau}_a$ against the reciprocal of the first-mover activations, $1/\langle n_a \rangle$,

such that

$$\rho^2 \left(\frac{1}{N\eta} + \tau \right) = 2\mu\beta \sin(\alpha). \quad (10)$$

Balance (10) offers a crude estimate of the parameter combination where the colony transitions from unsynchronized to synchronized activity.

Parametrizing by the crossover density is sufficient for approximating the position of the transition point when $s_0 \gtrsim 0.1$ (Fig. 6). For decreasing speed, balance (10) underestimates the true crossover density in the model, but it properly predicts that below $\mu \lesssim 0.5$ the model does not synchronize for any measured value of μ . The inability to synchronize for low density and temperature is likely due to the increased travel time between conspecifics, suggesting an increase in the difficulty for a first mover to form long-range cascading interactions when the nest is sparsely populated. The accuracy of balance (10) is further illustrated by solving for the deactivation rate [Fig. 7(a)]. Our estimate also holds across scales [Figs. 7(b) and 7(c)], where we demonstrate the crossover deactivation rate parametrized by β and τ . When $\beta \gtrsim 0.03$, and across the entire range of τ , the crossover ρ follows the change in the position of the peak in phase coherence.

IV. CONCLUSION

In this paper, we pose the following question: What characteristics of a complex system determine whether it will synchronize? In response, we present a model of ant activity that combines the well-known autocatalytic mechanism of Goss and Deneubourg [40] with empirically measured movement rules [49,50]. Our main findings are fourfold. First, the model exhibits activity bursts for biologically feasible parameter choices, whose values are derived from experimental observations in extant literature. Second, synchronization is the colony's response to excitement from a first mover, which cascades through the nest and creates the burst. Third, ant colonies live in a high-speed phase regime, where we can reasonably predict the onset of synchrony by comparing the expected timing of the activity burst with activations from a first mover. Finally, in the high-speed regime the phase transition occurs at a significantly lower density, owing to the improved, long-range spatial correlation created between conspecifics moving at speeds that are large in comparison to the burst timescale.

In studies of collective behavior, researchers often examine how information propagates through a group and influences emergent, system-level dynamics [37]. For example, in colonies of crazy ants (*Paratrechina longicornis*), Chatterjee *et al.* [74] established that the number of conspecifics participating in collective transport is fundamental to the responsiveness of the group: too many ants and the direction of the group is difficult to correct; too few ants and individuals compete to control the average heading. At an intermediate size, a single “leader” (an ant with information on the location of the nest) is capable of influencing the average heading of the group. In connection to activity bursts, these observations suggest that activity bursts in ant colonies are the result of a first mover (the “leader” of the burst) that

excites the colony in a synchronized regime, thereby favoring the rapid communication of new behaviors throughout the group.

Similar leader-driven cascades appear across a wide range of collective systems [38]. In herds of Merino sheep (*Ovis aries*), for example, one can observe intermittent clustering while grazing, whereby the herd transitions periodically between a high-density defensive group and a low-density foraging group [32]. Packing events (group-level transitions from low to high density) are initiated by a single individual (the “leader” of the packing event) that closes the gap between themselves and another sheep, exciting their neighbors until eventually the entire group becomes dense. Our results indicate that these cascades are governed by three key factors: the susceptibility of individuals to adopting a focal state (activity in ants or packing in sheep), the balance between time spent in that state versus quiescence, and the speed of the behavior transmission.

Under these premises, we may propose that systems that do not exhibit synchronized behaviors have individuals that (i) are resistant to the focal state (low β), (ii) are persistently in the focal state (low ρ or τ), or (iii) move slowly relative to the system's spatial scale (low s_0). Systems that have any of these characteristics may not be able to form the indirect, long-range interactions that are needed to facilitate the spread of the focal state. Partial support to this proposal can be garnered by examining results from Neves *et al.*, who found that *Pheidole rudigenis* workers do not synchronize their activity around any measurable rhythm [59]. We propose that this lack of synchronization can be explained as resistance to the focal state, based on the following grounding. The worker class of *P. rudigenis* ants are dimorphic, and they have well-known task separation between the minor class (small, general-purpose laborers) and major class (big-headed soldier ants) [75,76]. Existing studies demonstrated that recruitment of a major worker typically requires more stimulus than in members of the minor class [77], so that it is tenable that the colony is effectively governed by a low β .

Although the model clarifies how motion-driven mixing can generate colony-wide bursts, our analysis relies on choices that bound its quantitative scope: we make simplifying claims on the geometry of motion, use idealized contact rules, and do not represent heterogeneity in space or caste. Several parameters are also estimated at the colony level rather than individually, and there is no mechanism for perturbations to the colony. These choices allow for tractable analysis of the dynamics and intuitive predictions of the phase transition. However, it also means that comparisons between the various regimes and real data should be interpreted with caution.

Future work should seek to understand (i) the proximity of synchronized colonies to the phase transition and (ii) the adaptive purpose of the activity bursts, whereby we suspect that the responsiveness of the nest to information provided by individuals allows for a more efficient “call to action” when resources are low or a specific task needs completion. The first can be achieved by calibrating the model presented here to the motion of individuals from a single colony of ants while quantifying the activity dynamics of the colony as a whole. Validation can take the form of comparisons between

the phase transitions measured in the model and real colonies for variations in density and size.

Another important avenue for consideration is the generation of heterogeneous spatial effects in the model. Existing research demonstrates that colonies of ants create dense subregions surrounding the brood pile [78,79]. These clusters of ants create nontrivial spatial correlations in the activity [16] and contribute to energetic regulation as the colony grows in size [36]. The model presented here, however, maintains a homogeneous mixing assumption across the entire tested parameter range. This choice is largely due to the limited availability of spatial data recorded over time in ant colonies, suggesting a natural two-pronged direction for future extensions of our analysis. First, it is necessary to conduct experiments that gauge the dependence between activity rhythms and the spatial distribution of conspecifics. Second, spatial heterogeneity may be introduced into the model either directly (e.g., by imposing a negative correlation between the number of connections an ant has and its speed) or by identifying a parameter regime that supports clustering of immobile ants, possibly through variation of the social deactivation rate, γ . In experiments conducted by Boi *et al.*, spatially distinct groups within the nest were capable of synchronizing their activity bursts, owing to the transmission of ants between clusters [16]. We suspect that adding clustering to the model will leave the emergence of bursts largely unaffected, provided ants can navigate between clusters during activity stints.

By building an empirically grounded model of activity bursts that incorporates both movement through the nest and simple behavioral transitions, we are able to frame activity synchronization in a more informative context. Not only does the model inform researchers of the key features of ant behavior that allow bursts to emerge, but it also provides a guide for biologists to follow when constructing unique, informative experiments and highlights the importance of gauging the various timescales within the nest. Beyond biology, understanding the anatomy of activity bursts can inform the design of artificial distributed systems that require rapid, coordinated mobilization of agents. In systems where agents communicate locally but carry out tasks spread across a large space—for example, the navigation of robots performing tasks in a warehouse—decentralized mechanisms for synchronizing activity might enhance overall system productivity. In this light, our results suggest guidelines for calibrating such systems, providing engineers a method to exert an indirect control over the temporal behavior of the entire population of agents.

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DATA AVAILABILITY

All programs and simulation data needed to reproduce the analysis are available on GitHub [80].

APPENDIX A: DETERMINISM AS A METRIC FOR SYNCHRONY

Similar to $\mathcal{A}$, we compute the proportion of the population in the inactive and refractory states and construct a composition variable $\vec{y}(t) \in \mathbb{R}^3$ that represents the proportion of ants in the three subpopulations. We record $\vec{y}$ over T time steps with measurements taken every Δt units of time (which may differ from the simulation time step δt). A recurrence map M is then constructed by defining a threshold ε and connecting two points in discrete time t_u and t_q using the Heaviside function $\mathbb{H}(\cdot)$, such that

$$M_{u,q} = \mathbb{H}(|\vec{y}(t_u) - \vec{y}(t_q)| < \varepsilon). \quad (\text{A1})$$

Obviously, $M_{u,u} = 1$ for all u and the matrix is symmetric, $M_{u,q} = M_{q,u}$, for all combinations of u and q .

A useful metric in identifying the onset of synchronization will then be the determinism of the recurrence map, a quantity that reflects how predictable the underlying time series is over long periods of time. Determinism is defined as

$$\zeta(M; w_0) = \frac{\sum_{w=w_0}^{T-1} wW(w)}{\sum_{w=1}^{T-1} wW(w)}, \quad (\text{A2})$$

where $W(w)$ counts the number of diagonal lines of length w . Diagonal lines in M represent extended periods of deterministic behavior, and ζ is the ratio of the number of edges contained in a diagonal line to the total number of edges (see discussions by Goswami [61] for details). Computed over the time series describing activity, $\zeta \approx 1$ reflects either a constant level of activity or periodic oscillations. Careful selection of ε allows us to dismiss the former as a reason for high determinism, as ζ naturally decreases for phase-space trajectories stochastically varying around a mean. Determinism tells us whether the time series is predictable and allows us to make direct comparisons between time series, independent of their amplitude and frequency. For these reasons, high determinism can be associated with the emergence of activity bursts within the colony, and represents a “shape-agnostic” measure of synchrony.

For each time series, we construct the recurrence map using the proportion of ants in the three activity states (active, inactive, and refractory) and downsample it to a time step of $\Delta t = 5$ nondimensional units. We use the recurrence rate, $\kappa = \frac{1}{T^2} \sum_{u,q=1}^T R_{t_u,t_q}$, as a measure of the “likeness” of two recurrence maps and select ε so that the κ is consistent across simulations. We thus parametrize the recurrence map by ε and search for the value which yields $\kappa \approx 0.025$, which generally

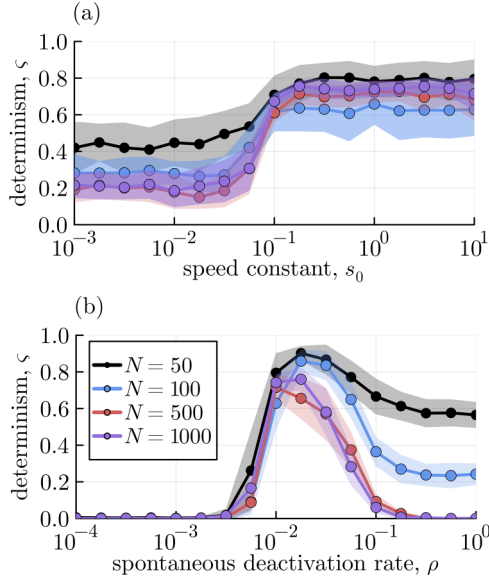


FIG. 8. Determinism as an alternative metric for synchronized activity. (a) We simulate the model for systems sizes $N \in \{50, 100, 500, 1000\}$ while varying the speed constant, $s_0 \in [10^{-3}, 10]$ (17 points). The remaining parameters are set according to the nominal values provided in Table I (fourth column) except those given by ranges, which are set equal to $(\mu, \rho, \beta, \tau) = (1, 0.01, 0.1, 750)$. (b) Likewise, we vary the spontaneous deactivation rate, $\rho \in [10^{-4}, 1]$ (17 points), keeping all parameters consistent with (a) except speed, which we set to $s_0 = 10$. In both cases, the model is simulated for 10^4 units of time (50 replicates) with the latter half being used to compute the mean determinism (solid curve) and standard deviation (shaded region). The transition from unsynchronized to synchronized behavior is consistent with that demonstrated by the phase-coherence metric, and points toward a robust parameter-driven phase transition.

occurs when $\varepsilon \leq 0.01$. Additionally, we adjust the minimum line length used to compute determinism to $w_0 = 10$ to neglect short periods of close trajectories in the phase space, which are found to occur in some cases even in the presence of a high degree of noise [60,61].

To demonstrate the determinism metric, we run simulations for $N \in \{50, 100, 500, 1000\}$ ants using the parameters defined in Table I (fourth column), with the parameters given by ranges set to $(\mu, \rho, \beta, \tau) = (1, 0.01, 0.1, 750)$. The model is simulated for 10^4 units of time, with the latter 5000 units of time used for analysis (50 replicates). This process is repeated for each speed constant in the range $s_0 \in [10^{-3}, 1]$ (17 points), and the resulting activity time series are used to compute the mean and standard deviation of the determinism, ζ (Fig. 8). For approximately the same threshold discussed in Sec. III B 1 the determinism transitions to a range indicative of a predictable time series, denoting a transition to a regime with activity bursts. The ability to capture the transition to synchronized behavior via both determinism and phase coherence speaks to the robustness of the two metrics.

Finally, we reproduce the peak measured in the phase coherence when varying the spontaneous deactivation rate, ρ , using the determinism metric. We simulate the model for system sizes for $N \in \{50, 100, 500, 1000\}$ ants and the

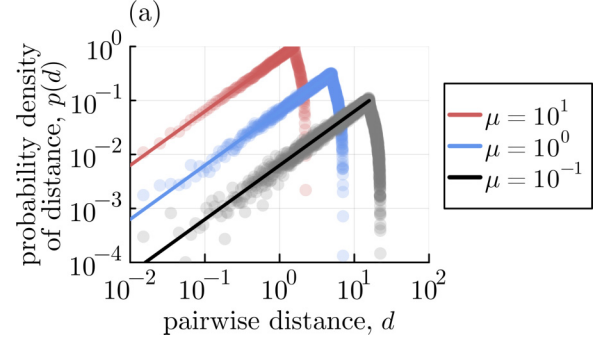


FIG. 9. Homogeneous mixing holds for variations in density, μ . We simulate the model while varying the system density $\mu \in \{0.1, 1, 10\}$ and compute in a simulation of $N = 100$ ants the pairwise distance distribution between individuals. Simulation parameters and computational details are otherwise synonymous with those discussed in Fig. 2. For each density, we measure a distribution consistent with homogeneous mixing as illustrated by the accuracy of the linear growth in probability, $p(d) = (2\pi/\ell^2)d$ (solid line), which extends to the edge of the maximal inscribed circle, $\ell/2$, before diminishing with an exponential-like tail toward $\ell/\sqrt{2}$.

nondimensional parameter values given in Table I (fourth column). With respect to the four parameters given by ranges in the table, we choose values corresponding to a high-speed regime, namely, $(\mu, s_0, \beta, \tau) = (1, 10, 0.1, 750)$, and for ρ we consider rates logarithmically spaced in $[10^{-4}, 1]$ (17 points). The determinism over the time series measures a similar peak to that seen in the phase-coherence case, highlighting the emergence of activity bursts for $\rho \approx 0.033$ in the high-speed phase regime.

APPENDIX B: INVARIANCE OF THE HOMOGENEOUS MIXING ASSUMPTION

To further illustrate that the homogeneous mixing assumption holds for variations in the system density, we vary the density across orders of magnitude, $\mu \in \{0.1, 1, 10\}$, with $N = 100$ ants and compute the pairwise distance distribution (Fig. 9). The remaining parameters are set to the values reported in Table I (fourth column) with parameters denoted by ranges set equal to $(s_0, \rho, \beta, \tau) = (5.869, 0.01, 0.1, 750)$. We find that variations in the density do not diminish the accuracy of the homogeneous mixing assumption, as denoted by the linear relationship between the probability and the distance, $p(d)$. We note that activity bursts did not emerge when $\mu = 0.1$.

APPENDIX C: EXPECTED WAIT TIME BEFORE A FIRST MOVER ACTIVATES

We are interested in the minimum wait time until a first mover activates in a population of inactive ants. Given the population is completely inactive, the next activation, which coalesces into a wave of activity in the colony, depends only on the spontaneous activation rate, η . The probability of an arbitrary ant to activate becomes $P(b \rightarrow a) = \eta$, and the time spent in the inactive state by a focal ant is described by a Poisson point process with probability density function

$p(t_{b \rightarrow a}) = \eta e^{-\eta t_{b \rightarrow a}}$, where $t_{b \rightarrow a}$ is the time until a focal ant transitions [53]. Being that the probability of transitioning spontaneously is independent for each ant, the wait time for the first activation is the closure of the exponential distribution

under minima, which is also exponential with rate equal to the sum of the rates in the underlying processes [53]. The new probability density function is thus written $p(t_{b \rightarrow a} | N) = N\eta e^{-(N\eta)t_{b \rightarrow a}}$ with the expected value $1/(N\eta)$.

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