Agitated ants: regulation and self-organization of incipient nest excavation via collisional cues

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1. Introduction

A variety of complex systems display collective behaviours [1–4]. These collective activities often originate through the process of self-organization [1,5,6]. Self-organization represents a remarkable phenomenon whereby individuals engage in relatively simple interactions leading to sophisticated, collective actions [2,7,8]. The emergence of collective behaviours through self-organization represents an important phenomenon across physical and biological systems and scales [1–3].

Highly social animals are key systems for studying collective behaviours. For example, highly social insects, which include all ants and termites, as well as some bees, wasps, thrips, beetles and aphids, are remarkable in their ability to coordinate activities and self-organize to behave as a single ‘super-organism’ [9–11]. The tremendous success of many social insects relies critically on the collective actions that lead to nest construction [10–19]. Nests provide protection and hospitable environments for rearing offspring [20,21]. Nests may also contain networks of tunnels and chambers used to house individuals and food [19,22–30]. In general, the social insect nest represents a fundamental part of the extended phenotype of the society [16].

The behaviours leading to the successful construction of nests by social insects are remarkable [7,12,31–36]. No single individual has a conception of how the nest should be built or what it should look like when completed...
Instead, social insects self-organize by using behavioural rules that lead to the formation of complex structures [1,3,5,34,38,39]. Higher-level nest patterns emerge from simple, lower-level interactions and environmental cues [3,7,31,34,35,39–41]. The evolutionary success of insect superorganisms such as an ant colony relies on adaptive regulation to manage competing priorities including safety, rest, hunger and reproduction [42,43]. Uncovering the mechanisms of coordination underlying such regulation is key to understanding social behaviour and serves as inspiration for protocols to be implemented in synthetic collectives.

A major goal of the study of collective behaviour is to understand the rules governing group activities. For example, during fresh nest excavation, it may seem straightforward that ants which cannot find existing tunnels would choose to dig new ones; however, it is not as obvious how ants collectively deprioritize excavation when a system of tunnels is sufficiently developed. Early nest excavation in ants and termites displays consistent rate regulation [44–46]. This has previously been attributed to a recruitment process and modelled using a logistic model, without mechanistic explanation [44]. More recently, Bruce et al. [45] suggested that ants regulate excavation rate through encounters in a manner that is collective-size dependent and sensitive to existing tunnels for small collectives. The excavated area over time was concluded to follow a Michaelis–Menten curve [47], suggestive of a self-inhibiting mechanism whereby the existence of excavated area inhibits further excavation. Bruce et al. interpreted their results as an indication that the ants attempted to minimize contact with each other; however, few studies have directly provided a window into the individual decision making and how it affects an emergent collective outcome.

Interactions between individuals could occur through a variety of communication mechanisms including chemicals, sound and contact. Underground and in the absence of light sources, vision is unlikely to contribute to individual interactions, as evidenced by the evolved blindness of termite soldiers [48]. Instead, chemicals, such as pheromones, are often cited as the dominant mode of communication for collective task regulation [48,49]. However, the proximate mechanisms used to convey information across biological collectives remain poorly understood.

The goal of this investigation was to gain a greater understanding of the dynamics underlying the successful excavation of nests in biological collectives. We wished to understand the proximate biological and physical mechanisms that ants use to regulate nest excavation, and to determine how various individual and group behaviours affect the overall dynamics. Our interest was specifically to determine if excavation regulation could emerge from independent individual decisions without invoking communication through chemical, visual or acoustic signals. Inspired by our recent studies on contact-responsive robotic collectives [50,51], we explored how contact sensing, as an information source, may contribute to global excavation regulation without other communication. To discover a minimal model, we make a simplifying assumption that ants make decisions based on their recent experiences, where encounters with others are registered but no information is actively passed between them. Our research makes use of experiments of ant excavation and subsequent mathematical modelling and computer simulation used to interpret the experimental results. Our models exhibit remarkable agreement with the experiments, suggesting that collectives can successfully rely on simple contacts to coordinate their group activities, and further, our model can generate testable predictions for further experimental studies.

2. Methods

2.1. Ant excavation experiment

We investigated substrate excavation dynamics in small groups of the fire ant Solenopsis invicta [52]. Solenopsis invicta ants are master builders. They successfully construct complex nests in soils or granular substrates found around the world using a diversity of materials [14,46,48,52–54]. The S. invicta nest is a complex, sophisticated structure that allows individuals to move and rear offspring. The nest is fundamentally important to the success of S. invicta colonies and is one of the most conspicuous features of this social insect.

Three colonies of S. invicta were collected from Atlanta, Georgia, USA during the fall of 2020. Individuals were separated from soil using the drip flotation method [55]. Collected individuals were then housed in plastic containers and supplied with water and food as needed to ensure their continued survival.

We sought to visualize the behaviours that S. invicta workers engaged in while excavating tunnels, to gain a greater understanding of the processes they use to construct nests. To do so, we monitored ant substrate excavation dynamics in experimentally created arenas, over many hours. Experiments were conducted inside set-up consisting of two areas accessible by the fire ants: an open entrance area to which ants were added for each trial and a digging area connected by a tunnel where excavation behaviours could be monitored through an acrylic wall (figure 1). The excavation arena consisted of a 195 × 145 × 2.5 mm³ quasi-two-dimensional space, defined by a three-dimensional-printed frame, to allow for monitoring of tunnel growth and ant activity. Glass particles measuring 0.7 ± 0.1 mm in diameter were used as an artificial substrate to be manipulated by the ants. Moisture content of the substrate was maintained at 10% water by weight across all trials; we have previously shown that S. invicta ants’ excavation rate is insensitive to moisture content in the range of 5–20% [56]. The walls of the arena and entrance area were coated with talcum powder to ensure that ants could not climb out of the designated spaces. During experimental excavation trials, a controlled number of ants were transferred manually from the collected colony to the digging arena. Non-warming LED light sources were directed at the digging area to offer illumination for recording.

We allowed groups of S. invicta workers to excavate within the artificial arenas. For each trial, groups of 40–70 randomly selected worker fire ants were transferred into the apparatus. In total, nine experimental trials were included in this study, using ants from three colonies, each used in at least two trials. Recording was started immediately following the addition of ants to the entrance area of the experimental set-up. Once introduced into the entrance, the ants were allowed to migrate independently down into the digging arena. Fire ant excavation in the digging arena was monitored and recorded for up to 70 h in each trial, which was recorded at 24 frames per second (fps) using a consumer computer camera (Logitech C920), at a resolution of 1920 × 1080 pixels.

2.2. Video analysis

To elucidate behavioural patterns involved in nest construction, we quantified collective excavation, ant spatial distribution, tunnel morphology, as well as individual ant–ant interactions, through manual and automated video tracking.
To estimate ant participation in excavation, we used captured colour differences to classify image pixels belonging to ants, as well as to detect the substrate interface. We used a bright green sheet as the background for the digging arena, which produced a visual contrast with the substrate, as well as with the ants; this contrast made for convenient video analysis based on colour differences (figure 2a,b).

Within our experiments, we defined ants as participating in some aspect of the excavation process if they were below the substrate interface. Once pixels were classified as belonging to ants below the substrate interface, the pixel count was converted to an estimate of the number of ants, using a calibration curve from a linear fit of manually counted ants versus detected pixel count, tabulated over multiple time points, for each recorded video.

We were interested in observing the excavation progression and rate regulation by detecting the excavated tunnels over time. This was done by following areas in the digging arena newly explored by the ants. Procedurally, we could accumulate a map of pixels that were classified as belonging to an ant at any given time in the past. However, the small amount of noise inherent in that technique, when accumulated, produces too many spurious detections of newly explored areas. Instead, we found that calculating and accumulating motion detection produced much less noise. To calculate motion detection, we down-sampled our videos in time to 12 fps by averaging subsequent frames, and then calculated the difference between the resultant frames. The result was then subjected to Gaussian filtering and a threshold was applied. The threshold was determined dynamically as five times the standard deviation of the Gaussian filtered values, over a region of the video determined to not have been excavated throughout the recording (manually). Figure 2c shows an example of motion-detected pixels, red (blue) indicates pixels that became lighter (darker) between successive down-sampled frames. A map of accumulated motion-detected pixels was recorded over each recorded trial.

Ants occasionally reversed and backed out of a tunnel when their path was blocked by other ants. Reversal is an important behaviour that minimizes traffic clusters [57] and we wanted to observe its relation to the number of ants in the tunnels and the overall excavation rate. We, therefore, tabulated counts of ants reversing without excavating a bolus of substrate material, following an encounter with another ant. This was done for several non-branching tunnels, in multiple experiments, by visual inspection.

### 2.3. Cellular automata model

To gain an understanding of the ant excavation dynamics, particularly in the earlier times of excavation, we employed a cellular automata (CA) model adapted from that in our previous work [57]. A CA model allows us to focus on the behavioural aspect, without a need to implement detailed mechanics of walking and digging. The simulation process boils down to a small set of time-evolution and interaction rules that are applied at every discrete step. Using this model, we may conveniently test various behavioural rules and then test how the CA model’s emergent collective behaviour matches experimental observations.

In the simulated system, ants walk through a linear tunnel that is composed of discrete cells that accommodate two ants each, going in either the same or opposite directions (figure 3). A tunnel has an entrance into a sequence of ‘substrate-free’ cells, followed by cells filled with substrate. At each time step (TS), ants move along the tunnel until they reach substrate; at which point they pause and excavate pellets. Once a substrate cell is drained...
As mentioned above, two ants may occupy the same cell and pass each other unhindered under this model. Three (or more) body collisions occur when an ant tries to move into a cell that is already occupied by two other ants. In response to such a collision, an ant that is heading towards the tip of the tunnel randomly chooses whether to reverse course without digging, with a predetermined probability. We find that our results are not sensitive to this reversal probability within the range (0.1, 0.9), and choose to fix this value to 0.34, as previously used [57]. An ant that is headed towards the exit never relents. In our previous work, we used only a single simulated tunnel [57], but here we use multiple tunnels to capture the observed experimental behaviour, as discussed below. Within the multi-tunnel CA model, when ants enter a tunnel, they first randomly and uniformly choose which of the multiple tunnels to go into. From there, the simulation proceeds as previously discussed.

2.4. Ant speed measurements
We analysed image maps to estimate an ant’s walking speed within tunnels. Given tracked exploration maps (figure 4), we extracted an example of a long branch-less tunnel and generated a linearized profile through the following steps: (i) fit a centre-line spline, (ii) generate perpendicular cross-sections at equal longitudinal intervals (figure 5a), and (iii) sum binarized pixel values across each cross-section. As ants walk through the tunnel, the linearized profile displays a travelling cluster of high values. We lay out these linear profiles over time as a space–time diagram (figure 5b,c). We then use a sliding time window of 1 min and for each window run a line-detection algorithm (figure 5). Ant walking speeds are captured as the detected line slopes. We accumulated the distribution of observed speeds for well-detected lines. Through thousands of detected slopes, we observed a mean speed of 0.27 ± 0.09 BL s⁻¹.

2.5. Model fitting
To fit the experimentally observed excavation rate, we iterated through randomly generated values for the free parameters of the simulated model and compared with the observed curves. Other fixed parameters have been determined either in previous work or in this study (table 1). The CA simulation time has been rescaled such that the ant nominal speed BL/TS is the experimentally determined mean ant walking speed. The model we fit then has four free parameters—number of tunnels, work–rest imbalance constant (n), relaxation length (L₀) and steady-state participation level (we discuss the meaning of these parameters in Section 3).

We started by generating 10 000 uniformly random sampled sets of parameters, in a wide range. To test a fit over multiple timescales, we first converted both the observed curve and each simulation curve to log-rate over log-time, by averaging within exponentially spaced bins and then taking the log of the average rate in each. The corresponding squared-error for each bin was taken to be the average of squared-errors, weighted by the number of observations. The error of the log-rate was taken to be \( \Delta r = \log(r) - \log(r') \), where \( \Delta \) is the error of the rate and \( r \) the rate.

For each simulation excavation rate curve, we calculated the average of squared differences from the observed curve, weighted by \( (\Delta r)^{-2} \). We compared the average of squared errors across the range of 0.5–35 h, as a measure of the quality of fit. In each refinement iteration, we used enough sampled parameter sets to display a clear trend in at least one parameter. Following each iteration we narrowed the search for those parameters that displayed a clear minimum (figure 6).

Figure 3. Cellular-automata simulation of ant excavation. Within this model, ants from the outside reservoir (circle on top) randomly decide to enter the system, with a probability determined by each individual. Once inside, the ants (blue half-arrows) move along a tunnel composed of discrete cells. Each cell accommodates up to two ants. An ant moves from the entrance (top) towards the substrate (bottom, in grey), but cannot move into the substrate. Once an ant reaches the first substrate cell, it removes (i.e. excavates) pellets from it, one every time step. After reaching its pellet holding capacity, an ant reverses and moves back towards the entrance to deposit the excavated pellets. Substrate cells are initialized to contain a consistent number of pellets, which are then depleted by the incoming ants. The number of pellets remaining in the first reachable substrate cell is indicated by the degree of filling of lighter grey. (a) Four consecutive time steps, showing four ants in a single tunnel, at first (time \( T \)) with one heading out towards the entrance, two on their way towards the substrate and one already at the substrate interface. At \( T+1 \), another ant reaches the substrate, and the third is a cell behind. Since the next cell is occupied by two ants, the latter ant, at time \( T+2 \), decides to reverse and head back towards the entrance without excavating. Also at \( T+2 \), an ant steps outside and increases the count of ants in the outside reservoir (number in circle). The ants at the interface remain there to excavate until either the cell is depleted or their individual capacity is full. (b) In a multi-tunnel model, ants from the outside reservoir randomly decide to enter, as before, and also randomly uniformly choose which tunnel to go into. Once inside, the dynamics are as in a single independent tunnel.

of its pellets, it becomes available for ants to walk into. In this way, the tip of the tunnel, where the substrate starts, elongates over time.

Within this computational model, a cell represents a single ant body-length’s (BL) worth of tunnel. Tunnels made by S. invicta generally converge to approximately two ant body-widths (BW) [46] and allow most ants to pass each other unhindered. We, therefore, take cells to represent an area of BL × BW and allow two ants to occupy each. At each TS, an ant will move to the next cell, if it is empty, and will thereby be moving at a speed of BL/TS. By quantifying the typical ant speed within tunnels, we relate the simulation timescale to the excavation experiment timescale. Within the simulation, we parametrize the number of pellets in a cell full of the substrate and the number of pellets an ant will excavate each time; these, respectively, represent the typical accumulated time it takes the ants to excavate a BL length of the tunnel, and the typical time spent at the tunnel tip by each ant.
3. Results and discussion

Our overall goal was to understand the mechanisms that animal collectives use to coordinate their activities. We investigated this issue by studying patterns of tunnel excavation in fire ant societies. We combined theoretical and empirical approaches to gain insight into the possible proximate mechanisms used by fire ants to accomplish important group tasks.

3.1. Ant excavation experiments

Our first aim was to gain insight into the rate of excavation of tunnels by the ant collectives. Following the introduction of ants into the system through the entrance chamber (figure 1), ants explored the container and went through a narrow hole into the digging arena in the lower chamber, in view of the camera (see Methods). We observed that all...
Figure 6. Least-squares ($\chi^2$) optimization of the model fit through random parameter sampling. In each iteration, we sampled thousands of parameter variations and calculated the mean-square distance between the simulated excavation-rate trend and the experimental one. We plotted $\chi^2$ distances versus each one of the fitted parameters (blue points), as well as an outline of their basin as a guide (black dashed line). After each such iteration we narrowed the search range for parameters with a clear single-minimum in their basin.

3.2. Participation trend

To investigate the apparent regulation of excavation rate over time, we suspected two possible modulated parameters—participation level in excavation and walking speed. A previous study showed a weak decay of walking speed in time [45], not significant enough to explain our observed excavation rate. Our limited observations of walking speed did not reveal any trend in time. By contrast, we quantified the collective participation level in excavation, and discovered a distinct trend.

At all times during an experiment, a significant portion of the ants was above the substrate and not actively participating in excavation. While above the substrate, many of the non-excavating ants were found in clusters. This aggregation behaviour has been reported in previous studies, for multiple ant species [44–46,59–61]. Approximately 2–3 h into each trial, participation in excavation peaks at approximately 50% (figure 8a). Coincidentally, roughly at the same time, the slow excavation-rate decay begins (figure 9b). At later times, the...
adapt to the removal of the most active workers by
formance [51]. In fire ants, it was reported that groups
unequal workload distribution and improved group per-
recently, we reported on the implementation of reinforce-
clogs and maintaining optimal traffic flow conditions.
long duration or unequal tendency to enter tunnels; an unequal tendency
initial phase there is almost constant excavation rate, followed by a rapid
decay, and at longer times a slower decay. (b) Area growth rate over
time, with colours as in (a). A consistent feature of rapid excavation appears
in all trials at the first few hours, followed by fast decrease in rate and a
sharp transition, leading to slow decay in rate at long times.
average participation trend appears to fluctuate around a mean
value of approximately 27.8% (green dashed line in figure 8a),
calculated as the average participation between 5 and 35 h; this participation rate is consistent with previous reporting [46]. The early peak in participation correlates with the initial high exca-
vation rate and its rapid decay, but then the rate decays further,
while, surprisingly, participation remains constant.

3.3. Cellular automata behavioural model
To probe the effect of individual dynamics on participation in exca-
vation and the emergent excavation rate, we built upon
our CA model simulations in [57] (see Methods). In our pre-
vious work, we experimentally resolved the activity of ants at
the individual level, while excavating a single tunnel, and
consistently observed a highly unequal workload distribution
among excavating ants [57]. In corresponding CA simu-
lations, individuals were initialized to have a preset equal
or unequal tendency to enter tunnels; an unequal tendency
to enter the tunnels was crucial for avoiding long-duration
clogs and maintaining optimal traffic flow conditions.
Recently, we reported on the implementation of reinforce-
ment rules in a collective of excavating robots that results in
unequal workload distribution and improved group perfor-
ance [51]. In fire ants, it was reported that groups
adapt to the removal of the most active workers by
upregulating the activity of others [57], though we do not
know what mechanism they use to accomplish that.
The model we developed (below) generates unequal
workload at any given moment, but the turnover between
ants equalizes the workload quickly, compared with previous
observations of persistent inequality over 12 h [57]. Notably,
in [57] (electronic supplementary material), some turnover
in levels of activity was also observed. This inconsistency
can be regarded as a level of abstraction, where we capture
the collective level of activity but not the workload distri-
bution. The collective rate of excavation, which is of interest
here, scales as the number of actively excavating ants, or
mean participation level, at low ant densities. Workload inequality—the individual deviations from the mean partici-
pation—is a second-order effect which we do not consider
in this work.
First, we compared unmodified CA model simulations
(figure 3a) [57], originally developed to reproduce excavation
in a single tunnel, to the observed experimental trend and
found the excavation rate trend produced by the CA model
was far below that actually observed (figure 9). Expanding
the CA model to include multiple independent tunnels sharing
an ant reservoir results in a higher excavation rate, where a
model with 10 tunnels captures the experimental long-time

Figure 7. Excavation area dynamics for multiple trials of S. invicta digging. (a) Area excavated over time in nine independent trials (coloured points), along with their average (black line). A clear trend emerges where at the initial phase there is almost constant excavation rate, followed by a rapid
decay, and at longer times a slower decay. (b) Area growth rate over
time, with colours as in (a). A consistent feature of rapid excavation appears
in all trials at the first few hours, followed by fast decrease in rate and a
sharp transition, leading to slow decay in rate at long times.

Figure 8. A varying fraction of the ant collective actively participate in exca-
vation at any time. (a) Tracked ant participation in the recorded experimental
trials. Each coloured line represents an individual trial. The average trend
(black) peaks around 50% and later fluctuates around constant participation
of approximately 27.8% (green dashed line). (b) CA model simulations with
varying implemented features. In both a single tunnel (blue) and multiple
tunnel models (green), the participation monotonically increases over time,
though faster for multiple tunnels. To the multiple tunnels we added a tend-
cy to rest and maintain a 27.8% work to rest ratio (orange). Once ‘agitation’ is added to the previous model on top of resting behaviour
(brown), it overrides the behaviour at short tunnel lengths which manifests
as a high participation peak, followed by a sharp fall.
average trend (figure 9). Interestingly, both the unmodified and multi-tunnel CA models already capture the experimental long-time decay trend (figure 9). This result suggests that the slow decay is an inevitable result of excavation in an elongating tunnel.

Our multi-tunnel CA model still did not capture the early time trend that coincided with regulated participation. Moreover, the participation of ants in excavation saturates at 100% in the CA model, regardless of number of tunnels and in contrast with the experiment (figure 8). We thus posit that a stable and low participation in excavation requires a self-limiting process. We observed in experiments that most of the ants above the substrate aggregated together in clusters of inactive individuals; this inactivity invoked the possibility of a resting behaviour. Therefore, we implemented a self-limiting process in the CA simulations, maintaining a fixed work-to-rest ratio. Setting α to be \( \alpha = \frac{L}{N/L^2} \), where \( L \) is a length constant. By defining an ant’s response this way, we obtain a unified view of collisions with other ants, as well as with the end of the tunnel.

The expected mean free path in any single tunnel is \( L/f \), where \( L \) is the tunnel length and \( f \) is the (expected) number of failed moves, cause by the tunnel end and cells occupied by two ants. A single ant in a tunnel will experience \( f = 1 \) failed moves, and will, therefore, estimate \( L \approx L \). In a mean-field calculation, \( f \) is expected to be \( L \cdot P(\text{two ants in one cell}) = L \cdot (N/L)^2 \), where \( N \) is the number of ants in the tunnel, which would result in \( L \approx L^2/N^2 \). This mechanism effectively has a quadratic sensitivity to the density of ants in the tunnels. In practice, our move success-rate estimator (\( f \)) implementation uses an exponential moving average with a memory time constant of \( 2L_0 \) to avoid infinitely long memory.

The result of this length-dependent relaxation mechanism is a higher tendency for the simulated ants to excavate at short tunnel lengths, overriding the steady-state work–rest behaviour. As the length of a tunnel increases, the participation of ants in excavation relaxes to its steady-state value.

Figure 9. Experimental and computer-simulated excavation rate over time. CA model simulation fit to the excavation rate (brown line) over the experimental average (black line) and its standard deviation (shaded). The fit was generated by a model including a mean free path dependent ‘agitation’ override. The same model was also run, for reference, without ‘agitation’ (orange line), also without resting behaviour (green line), and finally also without multiple tunnels (blue line, multiplied by 10). Both models, as well as the experimental trend, are consistent with a one-at-a-time (OAT) like \( t^{-1/2} \) asymptotic behaviour (red dotted line, scaled to match experiment at long times).
As noted above, the mean free path estimator is highly density dependent through three+ body collisions, since there is no penalty (delay) for two-body collisions in the simulation. At tunnel lengths reaching the designated relaxation length $L_0$, some ants decide to rest, which further reduces density in the tunnel, and as a result a cascade of relaxation into the steady-state behaviour occurs. This cascade gives rise to a sharp transition in excavation rate, closely matching the observed experimental trend (figure 9, blue line).

Our developed CA model captures the subtleties of observed collective ant excavation behaviour, and its success suggests a behavioural mechanism employed by the individuals. Parameter variation around the best-fit solution demonstrates the observed features associated with each parameter, and in particular—that the relaxation length ($L_0$) modulates the steepness of the transition between early and long-time stages (figure 10). In figure 10(a), we observe a scaling of the curve for more than 15 tunnels, but a qualitatively different trend at early times for 10 tunnels. This qualitative change highlights the necessity of many tunnels to alleviate traffic congestion and achieve the high excavation rate at early times. Branching is prevalent in the experimental trials at early times (figure 4), and probably increases the effective number of tunnels needed for the CA model to match. In figure 10(b), we show that the steady-state participation level does not affect early times, as a result of the ‘agitation’ override. The overall response to varying $L_0$ in figure 10(c) is nonlinear and saturates at a value of 10 due to the nonlinear dependence of the mean free path in the density of ants in the tunnel, and the mechanism of its estimation by the modelled ants.

It is worth noting that our ‘agitation’ override captures previous concepts of ‘arousal’ and initial tunnel-length effect. The model also predicts faster relaxation with fewer ants, as fewer ants would result in fewer collisions for the same number of tunnels. Whether they would relax faster or not depends on the actual number of tunnels they generate, which may be affected by the width of the arena.

In this work, we introduced a resting mechanism employed homogeneously by all simulated ants, which results in a nearly equal workload distribution (data not shown). This is in contrast with previous findings of unequal participation in work and the potential rules leading up to it [51,57]. Our focus in this work was on emergent global regulation, rather than emergent workload distributions. The CA model here essentially captures the same global inequality as low participation rates at any moment, but the work is spread among all individuals. The same can be implemented with an unequal workload, by setting target work-to-rest ratios heterogeneously among the simulated individuals.

### 3.4. The one-at-a-time model

We turn our attention back to the seeming inevitability of the long-time excavation rate decay, which appears in experiment as well as in all of our CA model variation. Ants working inside a narrow tunnel can be considered as one-dimensional asymmetric exclusion processes with few lanes [57,62,63]. Let us consider an unregulated excavation-rate behaviour with a single ant, digging in a single tunnel. This ant performs a consistent walking and excavation procedure over time, going back and forth, digging at the tip of the tunnel and depositing dug pellets at the entrance (figure 11). We call this scenario the one-at-a-time (OAT) model, which we found experimental support for [57].

In this scenario, each digging cycle takes a time of $(2L/v) + \tau_{dd}$, where $L$ is the tunnel length, $v$ is the ant moving speed and $\tau_{dd}$ is the time it takes to manipulate the substrate while digging and depositing at either end of the tunnel.
tunnel. The average excavation rate for $K$ non-interacting ants will then be $\frac{dL}{dt} = K/(2L/v + \tau_{sd})$.

The corresponding tunnel growth follows the length–time relationship: $L(t) = \frac{1}{2} \left( -v\tau_{sd} + \sqrt{v^2\tau_{sd}^2 + 4KLt} \right)$, where the initial condition is set to $L(t=0)=0$. By taking the long-time limit $t \rightarrow \infty$ we see that in the OAT model, the tunnel length asymptotically grows as $t^{1/2}$, and by taking the long-time limit $t \rightarrow \infty$ we see that in the OAT model, the tunnel length asymptotically grows as $t^{1/2}$, and by taking the long-time limit $t \rightarrow \infty$ we see that in the OAT model, the tunnel length asymptotically grows as $t^{1/2}$, and the corresponding tunnel excavation rate follows $1/L \propto t^{-1/2}$ at long tunnel length or late time. Though this was derived for an ideal situation, it clearly extends to any scenario with a constant number of participating ants and negligible time spent on collisions or any activity other than walking and manipulating substrate. Remarkably, this derived long-time rate trend agrees with both experiments and the CA model (figure 9, red dashed line). We posit that our observation of an OAT-like trend at long times (figure 9) is most likely a consequence of negligible interactions between active ants and a stable participation level, which our CA model generates.

4. Summary and conclusion

The goal of this study was to understand the dynamics of excavation behaviour by collectives of ants as model social insects which regularly confront crowded traffic conditions in a confined space. We performed ant excavation experiments in a quasi-two-dimensional system and observed a pattern of excavation-rate modulation [44,45,60]. Our experimental excavation rate trend reveals signs of regulation across timescales, including a high and constant initial rate, a fast decay, and a slow decay at long timescales (figure 7).

We developed a detailed, behavioural, CA model, carefully motivated and with most of its parameters derived from independent observations. Our model captures the experimental excavation rate trend very well across timescales, and suggests ants modulate their participation in excavation based on their recent history of collisions. Crucially, this modulation, which we refer to as an ‘agitation override’, addresses observed effects of both initial tunnel length and ant group size, and serves as a mechanistic description of the concept of ‘arousal’ which is referred to in [45].

Previous studies employed empirical models such as a logistic model or a power-law to describe their excavation rate observations without being clearly motivated by behavioural rules at the individual level [44,45,60]. We derive a quantitative fit, by introducing resting behaviour, which can be overridden in a state of agitation. Both the regulation of work–rest and agitation is done by each individual in our model. Agitation is determined from length estimates based on collisions with others, as well as with the end of the tunnel. Moreover, we showed that an idealized ‘one-at-a-time’ model, derived by considering the fundamental timescales in the system, predicts that the excavation rate at long times should decay like $t^{-1/2}$. This prediction fits our experimental observation and expectations at long timescales surprisingly well.

Our models do not include many aspects of the tunnel system, such as width variations, formation of branches, and unequal investment in the excavation of each tunnel. Despite that, the success of CA models in this (figure 9) and previous work [57] is promising, and could be extended to include other behaviours and additional details. We propose that CA models with similar rules might be applied to other social insects that perform tasks in crowded confined environments.

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Data accessibility. Relevant data and code are available at Figshare: https://doi.org/10.6084/m9.figshare.22649689.v1 [64].

Authors’ contributions. R.A.: data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; K.O.A.: conceptualization, investigation, methodology, writing—original draft; C.J.D.: conceptualization, investigation, methodology, writing—original draft; H.-S.K.: conceptualization, formal analysis, investigation; M.D.B.: conceptualization, formal analysis, methodology; M.A.D.G.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, writing—review and editing; D.I.G.: funding acquisition, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing.

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