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Excavation and aggregation as organizing factors in de novo construction by mound-building termites

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Termites construct complex mounds that are orders of magnitude larger than any individual and fulfil a variety of functional roles. Yet the processes through which these mounds are built, and by which the insects organize their efforts, remain poorly understood. The traditional understanding focuses on stigmergy, a form of indirect communication in which actions that change the environment provide cues that influence future work. Termite construction has long been thought to be organized via a putative ‘cement pheromone’: a chemical added to deposited soil that stimulates further deposition in the same area, thus creating a positive feedback loop whereby coherent structures are built up. To investigate the detailed mechanisms and behaviours through which termites self-organize the early stages of mound construction, we tracked the motion and behaviour of major workers from two *Macrotermes* species in experimental arenas. Rather than a construction process focused on accumulation of depositions, as models based on cement pheromone would suggest, our results indicated that the primary organizing mechanisms were based on excavation. Digging activity was focused on a small number of excavation sites, which in turn provided templates for soil deposition. This behaviour was mediated by a mechanism of aggregation, with termites being more likely to join in the work at an excavation site as the number of termites presently working at that site increased. Statistical analyses showed that this aggregation mechanism was a response to active digging, distinct from and unrelated to putative chemical cues that stimulate deposition. Agent-based simulations quantitatively supported the interpretation that the early stage of de novo construction is primarily organized by excavation and aggregation activity rather than by stigmergic deposition.

1. Introduction

Social insects are capable of a wide range of collective phenomena in which the group’s abilities are greater than those of any individual [1–3]. Among the most remarkable of these is the nest-building of termites, ants, bees and wasps [1,2]. Termites in particular construct complex mounds that are orders of magnitude larger than any individual, contain an intricate network of tunnels, and fulfil a variety of functional roles such as protecting against predators, facilitating gas exchange, and controlling water loss [4–7]. The ability of termite colonies to construct these mounds without any centralized leadership has inspired numerous inquiries into their individual and group behaviours.

Many theories of self-organization emphasize the role of stigmergy, a process of indirect communication through which individuals respond to features in the environment that result from other individuals’ previous labour [1,2]. Stigmergy plays a role in coordinating self-organized behaviours such as foraging, trail

formation and brood sorting [1,2], and is often mediated through pheromones (chemicals released by animals that generate responses by conspecifics).

Grassé was the first to suggest that stigmergy plays a key role in the self-organized construction of termite mounds [8]. In his seminal investigation of how termites build coherent structures, Grassé found that construction proceeds in two phases: first, an uncoordinated phase in which deposition (i.e. building with masticated soil pellets) occurs in scattered locations, followed by a coordinated phase in which deposited material accumulates at a few sites. Grassé proposed that workers coordinate where to build through a putative 'cement pheromone' that they add to deposited soil and that triggers others carrying soil to deposit on top or nearby. This process creates a focal positive feedback loop, allowing coherent structures to emerge without any direct coordination. Bruinsma later published an extensive examination of the termite construction process that provided further support for the stigmergy hypothesis [9]. In this commonly accepted explanation, excavation and deposition are uncoupled as termites transport soil pellets, potentially far from their source, until triggered by cement pheromone to deposit them.

A challenge to studying this collective construction process has been that technological limitations prevented researchers from tracking each individual's behaviour to determine how collective outcomes emerge from individual actions. Many researchers have therefore approached such systems through simulations. Based on the experimental results of Grassé and Bruinsma [8,9], many biologists and computer scientists have developed computational models of termite construction to evaluate self-organized building processes coordinated through stigmergic responses to a cement pheromone [1,2,10–14]. Given the limited empirical support from behavioural studies for the details of such models [10], however, these simulations should be interpreted as demonstration that coordination based on a hypothesized cement pheromone is *capable* of generating self-organized construction, rather than evidence that it necessarily does.

Two recent developments suggest the need for and ability to conduct new investigations into the mechanisms that termites use to coordinate mound construction. First, a number of recent studies have not found evidence for the primacy of a chemical pheromone—often suggesting alternative mechanisms—and thereby question the interpretations of Grassé and Bruinsma's original empirical investigations [15–18]. Second, advances in video recording and computer vision technologies have enabled the tracking of individuals within groups over the duration of experiments [19], yielding novel insights regarding behaviours and social structures within a wide variety of animal species [20,21]. In this study we take advantage of these technological developments to acquire more precise data about termite behaviour than has previously been possible.

The goal of this study is to examine the process of de novo construction among termites, and to characterize the mechanisms that termites use to coordinate this process. In particular, we aim to investigate whether a cement pheromone mechanism is sufficient to explain the process of self-organized termite construction or whether alternative mechanisms are necessary. We observed de novo construction by *Macrotermes michaelseni* and *Macrotermes natalensis* major workers in laboratory settings similar to those used in the studies of Grassé and Bruinsma, placing small groups of termites in Petri dishes

containing an initially featureless layer of soil. In order to analyse how the group coordinates construction, we characterized individual termites' behaviours and responses to a variety of cues such as the presence of excavation sites, the activity of other termites, individual histories of past activity, and species.

Classic models of termite construction emphasize that termites are stimulated by a putative cement pheromone to deposit pellets in the vicinity of recent depositions, but predict no particular pattern in where termites obtain soil, nor associations between where soil is excavated and where it is deposited. By contrast, our preliminary qualitative observations of de novo construction activity showed termites focused on digging in groups at large quarries and rarely carrying soil away. While the structures that emerged were similar to those identified in traditional models, they were all located along the edges of these quarries, suggesting that excavation plays a key role that should be interrogated further. We therefore hypothesized that mechanisms related to excavation, rather than deposition, enabled groups of termites to coordinate their early building activity. In particular, we hypothesized that the strongest influences on termite digging activity would be the location of existing excavation sites and the presence of actively digging termites, and that termites would respond more strongly to these features than to a putative chemical trace. A classic cement pheromone-based model would predict only deposition being influenced, and only by past deposition.

2. Methods

We conducted experiments in April 2015 at the Cheetah View Field Biology Station near Otjiwarongo, Namibia (20°25' S, 17°4' E). We studied six colonies of termites from the genus *Macrotermes* (Termitidae, Macrotermitinae), which are renowned for constructing complex mounds that are typically metres tall [4–6]. We investigated two *Macrotermes* species, *M. michaelseni* and *M. natalensis*, gathering termites from three mounds of each. While individuals from the two species are morphologically virtually indistinguishable, the mounds built by each species differ notably: *M. michaelseni* mounds are tall and narrow while *M. natalensis* mounds are short and broad (figure 1) [4]. We identified each species by the shape of the mounds, following the approach used in previous studies (E. Marais 2016, personal communication).

For each experiment, soil was obtained from an active building site ('fresh build') from the termites' own mounds (to match texture), cleaned with acetone (to remove any organic compounds), and thoroughly rinsed with water. We poured a thin (approx. 4 mm) layer of soil mixed with water into empty Petri dishes, and let it dry fully. Water was then added until the soil had a moisture level of 20% (by weight), the same level measured (through both weighing and using a soil moisture meter) in the fresh build. Each experiment placed 25 major workers into such an arena [16,17]. These arenas were contained within an acrylic box that eliminated airflow, and were filmed from above for an hour after the termites were introduced (figure 1; electronic supplementary material, video S1). Experiments for each colony were performed across multiple days, with all experiments performed within a period of 10 days.

We used custom video processing software to track termite positions and behaviours (electronic supplementary material, S1 and figures S1 and S2). The user seeded the tracking program at the desired starting frame of each video by manually marking the body and head positions of each termite. The semi-automated program then followed the body and head positions of each termite throughout the trial, prompting the user for manual



Figure 1. Overview of experimental preparation and set-up. (a) *Macrotermes michaelseni* mound (height approx. 3 m). (b) *Macrotermes natalensis* mound (height approx. 1 m). The two tubes sticking out of the mound are traps to collect termites and soil. (c) A typical arena at the end of the tracked period. This arena has three excavation sites—at the top, along the left edge, and on the bottom—with multiple termites working at each. The base of the dish (white) is visible at all three sites, indicating that the termites have dug all the way to the bottom of the soil layer. Large clusters of depositions are visible along the edges of each excavation site. (d) The laboratory set-up for running experiments. Petri dishes with soil and termites were placed inside a clear acrylic box, along with a ruler and thermometer/humidity meter. Experiments were filmed from above using iPod Touches. Two LED lamps illuminated the arena; light was diffused by placing a light tent (visible in the bottom left of panel) over the acrylic box. (e) An excavation site at the end of an hour-long trial. The borders of the excavation sites contain clusters of depositions, often forming pillars, displaying how excavation sites form a template for the emergence of structures. (Online version in colour.)

intervention to ensure accuracy and correct any self-detected errors (electronic supplementary material). Tracking covered a period from 3 min before initiation of the first excavation site (i.e. when the first termite began to dig up soil from the initially smooth layer, creating an excavation site at that location) until 10 min after that first initiation (or until termites disappeared under the soil, making tracking impossible).

Based on the activity observed in these experiments, we classified termite actions into two behaviours: wandering/resting (stationary or moving through the arena without altering any soil) and excavating/depositing (digging out soil and placing it nearby) (electronic supplementary material, video S2). We manually marked the borders of excavation sites in each arena; excavation and deposition events were identified as candidates by the automated software (based on entering/exiting excavation sites) and then manually verified. This process resulted in trajectories identifying the positions, orientations and behaviours of each termite at every 0.1 s during the tracked periods, allowing us to precisely study the behaviours of individuals and groups. We obtained trajectories on 396 termites across 18 experiments, for a total of 4067 min of tracked behaviour (we excluded from tracking 54 termites that remained stationary during their entire trial).

We considered a variety of environmental stimuli and individual traits that may influence when termites join excavation sites and how long they remain engaged there (table 1; electronic supplementary material, S1). One category of potential factors comprised traits of individual sites: the number of excavators at a site when a termite encountered it and the total time of excavation activity that had occurred there (a proxy for the size of the

site as well as the quantity of any chemical signal that termites might leave while working) [22]. Each termite's past interactions with the site were also considered, to determine if termites acted differently at sites they initiated or at which they had previously worked. We also accounted for the traits of individual termites, as termites exhibited considerable individual variability in overall time spent moving or digging. Together, these factors capture many potential mechanisms that could influence termite construction behaviour including stigmergy (via cumulative site activity), aggregation (via number of termites currently excavating), memory (via individual history of past excavation at this and other sites) and individual variation (via individual excavation propensity and mobility level).

We incorporated all of these factors as fixed effects into linear and generalized linear mixed models (LMMs and GLMMs, respectively) that included random effects for colonies, trials and individuals (electronic supplementary material) [23]. We developed statistical models to determine which factors influence the following three behaviours related to de novo construction: initiating new excavation sites (analysis 1; GLMM), joining existing excavation sites (analysis 2; GLMM), and the length of time spent excavating at a site (analysis 3; LMM). Because we do not know *a priori* which features impact termite behaviour, we performed model selection via backward selection, using the Bayesian information criterion [24] to find the most effective parsimonious model.

As a further check to explore how well different possible organizing mechanisms captured the patterns of excavation and deposition we observed during de novo building, we created

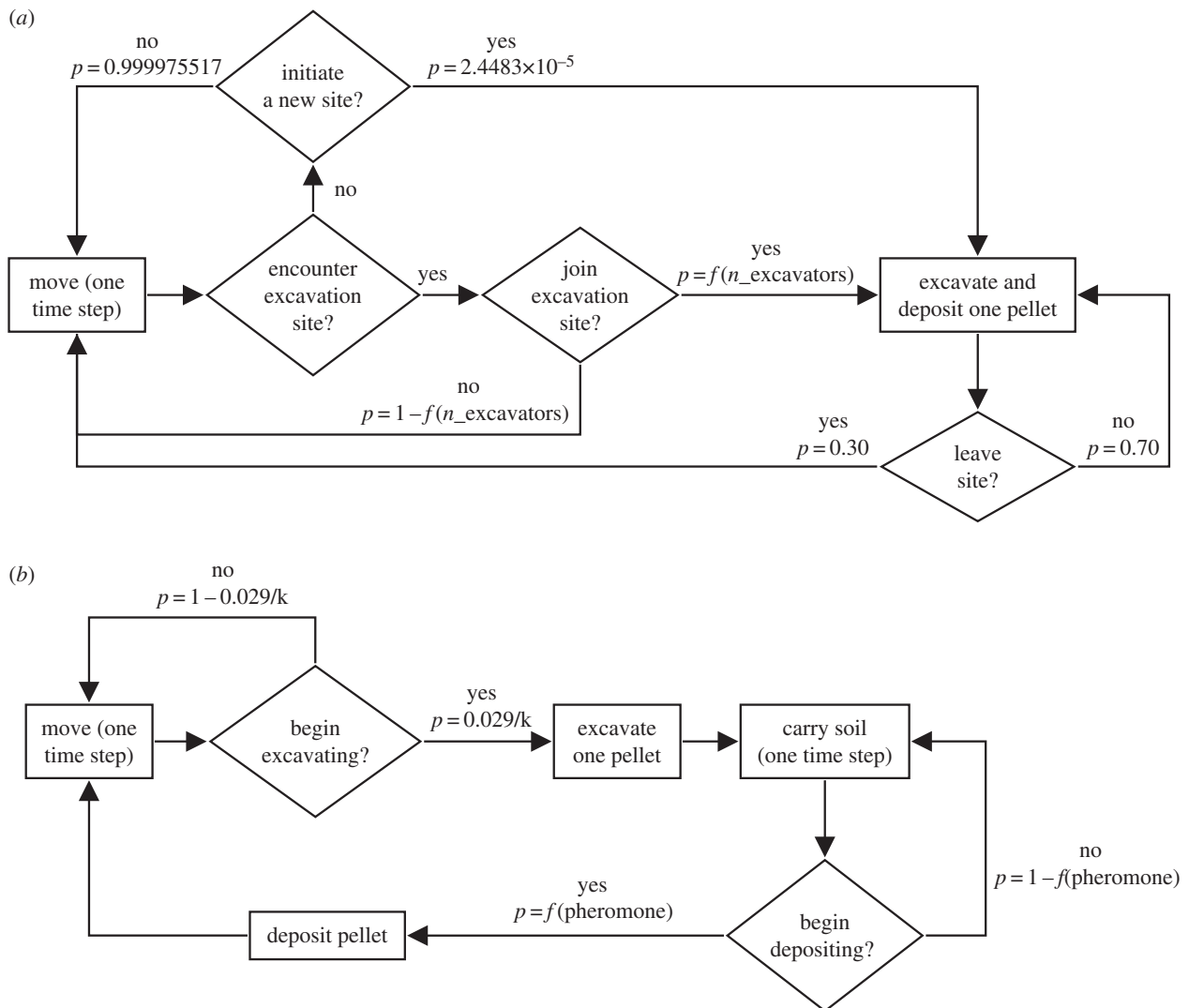


Figure 2. Behavioural models of termite construction behaviour. (a) Excavation model flowchart. (b) Pheromone model flowchart.

Table 1. Definitions of individual features and external stimuli considered in our analyses.

factor	description
excavation propensity	The total amount of time the termite spent excavating during the experiment.
mobility level	The total distance the termite travelled during the trial before the first initiation occurred.
<i>Macrotermes natalensis</i>	Is the termite an <i>M. natalensis</i> ?
previous excavation at any site	Has the termite previously excavated anywhere?
previous excavation at site	Has the termite previously excavated at this site?
site initiator	Did the termite initiate this excavation site?
number of termites	The number of termites currently excavating at the excavation site.
cumulative site activity	The total amount of time spent excavating by all termites at this excavation site so far.

two simple simulation models: (i) in an 'excavation model', based on our experimental observations, termites join excavation sites based on the number of termites working there and deposit excavated soil along the edges of quarries (figure 2a; electronic supplementary material, SI). Initiating and leaving excavation sites were modelled as stochastic behaviours, with fixed probabilities based on our observations (electronic supplementary material); and (ii) in a 'pheromone model', based on classic cement pheromone models [1,2,10–14], termites pick up soil pellets at random and are triggered by a cement pheromone to deposit them based on the number and recency of previous

depositions in their vicinity (figure 2b; electronic supplementary material). Parameter values for this model were chosen following a study with *Lasius niger* [10], a species that builds similar initial structures as do *Macrotermes* spp. and for which such a behavioural model was developed with parameter values obtained from experimental observation (electronic supplementary material). While neither model attempts to capture every observed element of termite behaviour, evaluating the overall patterns of excavation and deposition generated by these simulation models, and comparing them to the patterns that we observed in experiments, helps compare the importance of these two proposed mechanisms.

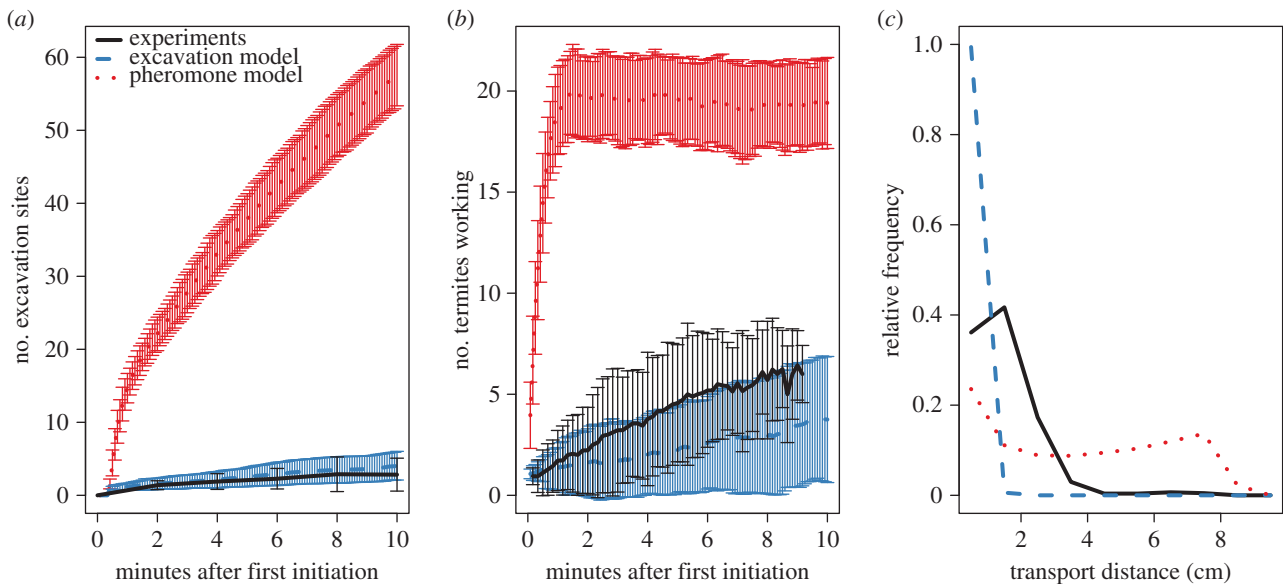


Figure 3. Key statistics from the experiments, excavation model and pheromone model. (a) The number of excavation sites over time. (b) The number of termites actively excavating over time. (c) The relative frequency of transport distances.

Simulations took place in a circular arena the same size as in the experiments (87 mm diameter, soil 4 mm deep); individual soil pellets were represented as cubes 1 mm on all sides. Termites were represented as 8×3 mm rectangles, and moved according to a motion model based on the termites in our experiments (electronic supplementary material, S1). We ran 100 iterations of each simplified model, tracking the building process for 10 min following the first initiation of an excavation site, and evaluated the models via the number and distribution of excavations, termite behaviour distribution, and pellet transport distances, comparing simulation results to experimental observations.

3. Results

(a) Excavation as the critical organizing behaviour

Excavation proceeded in two stages: a disorganized phase in which termites explored the arena and a few dug out individual soil pellets, followed by an organized phase in which coordinated excavation occurred at a few common sites (electronic supplementary material, video S3). During this second phase, the collective excavation activity within each arena was focused on a few regions, creating quarries where in places enough soil was removed to expose the bottom of the Petri dish (figure 1). These excavation sites often occurred along the borders of the arena, possibly because of the tendency for termites to follow along the wall of the arena, or because it may be easier to dig in the acute angle formed by the soil pad and the wall of the dish. Ten minutes after the first excavations, dishes contained on average 2.8 ± 2.4 (median = 2) distinct sites (figure 3).

We used the individual trajectories collected from our experiments to analyse the process through which this pattern of excavations emerges. A first observation is that initiating new excavation sites is a rare event. As the arenas are initially covered in a smooth layer of soil, a termite must initiate each excavation site. Out of the 396 termites tracked in our experiments and the 185 of those who excavated at some point, only 34 termites initiated excavation sites.

Engaging in excavation at existing excavation sites was far more common, and divisions of labour emerged within the

colonies. Approximately half (185 out of 396) of the termites engaged in excavation, often doing so for extended periods of time. We refer to these termites as ‘excavators’, and define excavation events as discrete periods during which a termite is actively working at a site without leaving. Overall, excavators worked on average 38% of the time between the first initiation and the end of the trial (electronic supplementary material, figure S5a; the excavation times can be described as an exponential distribution with decay rate 0.26 min^{-1} , standard error 0.19). There were 271 excavation events across the eighteen trials, lasting 94.5 s on average with a median time of 49.7 s (electronic supplementary material, figure S5b; an exponential distribution with decay rate 0.63 min^{-1} , standard error 0.04). Many of these (120 out of 271) lasted longer than a minute; the longest continuous excavation lasted over 7 min. A few key individuals were responsible for much of the work: the most active 25% of excavators were responsible for 52% of the total excavation time. The majority of termites did not excavate at all and were for the most part inactive during the trials.

Termites working at excavation sites deposited soil pellets almost exclusively along the border of the site. We found an overall mean value of 1.5 cm for the linear distance a pellet was moved between excavation and deposition (electronic supplementary material). Out of approximately 1040 depositions during the course of our experiments, in only 35 cases (3.4% of all depositions) did termites carry a pellet beyond the vicinity of an excavation site. An hour after termites were introduced into the arenas, pillars or arches had appeared in five out of the eighteen trials. Clusters of depositions were visible along the borders of excavation sites in the other 13 trials as well, albeit smaller and more amorphous. In every case where structures emerged they were at the edge of excavation sites, with the arches spanning across excavation sites from one edge to another.

(b) Factors influencing excavation behaviour

Our first analysis considers factors impacting whether each termite initiates excavation sites. Our results indicate that only excavation propensity is a predictor of which termites initiate

Table 2. Statistical results analysing the cues and traits that influence termite behaviours. (Analyses 1 and 2 represent binary decisions, and were computed using GLMMs (with the binomial family). We report the fixed effects as odds ratio (the proportional increase in odds given a one-unit increase in the factor); the direction of influence is indicated by whether the odds ratio is greater or less than 1. Analysis 3 has a linear response variable, and was computed using an LMM; the direction of influence is indicated by whether the coefficient is greater or less than 0. Three stars (***) indicate that the factor's *p*-value was less than 0.001, while two stars (**) indicate that the factor's *p*-value was less than 0.01; all factors included in the model were significant with *p*-value less than 0.01. For the random effects we report the standard deviation (st. dev.) of the coefficients. n.a. indicates that this feature is not applicable to a particular analysis. Dashes (—) indicate that model selection removed this feature. We do not report any of the interactions between species and the other fixed effects, as model selection removed these in every analysis.)

fixed effects	analysis 1: does the termite initiate a site?	analysis 2: does the termite join an excavation site it encounters?	analysis 3: how long does the termite remain excavating? (min)
(intercept)	2.58×10^{-3} (***)	1.47×10^{-4} (***)	0.84 (***)
excavation propensity (min)	1.79 (***)	4.21 (***)	0.43 (***)
mobility level (cm)	1.02 (**)	1.02 (**)	—
number of termites	n.a.	4.12 (***)	—
cumulative site activity (min)	n.a.	1.22 (***)	−0.03 (***)
previous excavation at site	n.a.	—	—
previous excavation at any site	n.a.	—	−1.15 (***)
site initiator	n.a.	—	−1.18 (***)
<i>Macrotermes natalensis</i>	—	—	—
random effects (st. dev.)			
colony	0.55	1.17×10^{-4}	0.13
trial	0.88	2.36	0.17
individual termite	n.a.	1.55	0.00
model fit			
χ^2	86.502	672.93	231.52
<i>p</i> -value	$<2.2 \times 10^{-16}$	$<2.2 \times 10^{-16}$	$<2.2 \times 10^{-16}$

new excavation sites (table 2, analysis 1): termites that are more active excavators throughout a trial are also more likely to initiate sites. Each minute of additional excavation increases a termite's odds (the likelihood of performing the action divided by the likelihood of not performing the action) to initiate a site at some point during the experiment by a factor of 1.79. We did not identify any factors influencing the locations of initiations; in other termite species, small depressions in tunnel walls act as cues for the initiation of excavation [25].

Our second analysis evaluates which features influence termites to join an excavation site that it encounters. Our results indicate that the key features determining whether a termite will join an excavation site are its excavation propensity and the number of other termites actively engaged at the site when it arrives (table 2, analysis 2). Every additional minute a termite spends excavating during a trial corresponds to a 4.2-fold increase in the odds of joining any specific excavation site it encounters; every additional termite working at a site increases the odds of a passing termite joining the work there by 4.1 times. We also observed positive effects for the amount of work that had previously occurred at the site, with every additional minute of past activity at a site increasing a termite's odds to join that site by a factor of 1.2.

To further evaluate the particular influence of the number of termites working at excavation sites in prompting others to join, we evaluated a subset of times that termites encountered excavation sites that were similar in all respects except for the presence or absence of other termites at the site. We

controlled for individual memory, site size and possible chemical cues by selecting all instances where a termite came across a site that: (i) it had never previously encountered, (ii) had received at most 1 min of total excavation, and (iii) had been excavated at within the last minute. In the 78 such cases where there was at least one other termite active at the excavation site, the termite joined the excavation site 27% ($n = 21$) of the time. In the 41 such instances where there were no other termites at the site, the termite never joined the excavation site. In fact, across all eighteen experiments ($n = 333$ cases), there was not a single instance where a termite encountering an excavation site for the first time started working when there were no other termites actively engaged there.

Our third analysis tested the factors that influence how long termites remain at excavation sites, and found that that duration depends on multiple factors (table 2, analysis 3). Termites with large excavation propensities stayed working at excavation sites for longer than those with smaller excavation propensities. On the other hand, termites that had initiated that same site or had previously excavated at any site stayed for shorter periods of time (both features corresponded to excavations that lasted 70 s shorter). The latter results indicate that a termite's past behaviour has an impact on its present behaviour. Interestingly, although the presence of other termites is a critical feature in attracting termites to join excavation sites, model selection did not include it as a factor affecting how long termites stay there. Model selection also removed all species differences, as it did with the other analyses.

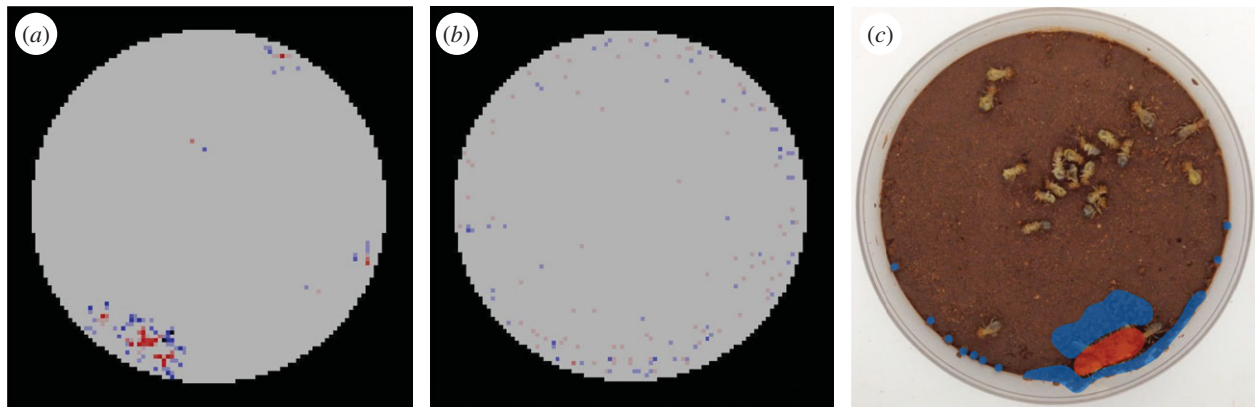


Figure 4. Typical outcomes from the excavation model, pheromone model and experiments. (a) The end of an excavation model simulation. (b) The end of a pheromone model simulation. Grey represents the base layer of soil. Red and blue represent excavation and deposition locations, respectively, with darker shades identifying a larger extent of digging (i.e. deeper) or building (i.e. taller). (c) The end of an experiment, with excavations marked in red and depositions in blue. See the electronic supplementary material, figure S6 for more examples.

(c) Agent-based simulation models

Figure 4 displays typical outcomes from the two simulation models compared with a typical end state from our experiments, with the excavation model producing arenas that resemble the experiments far more closely than the pheromone model does (electronic supplementary material, video S4 and figure S6).

Ten minutes into the building process, pheromone model simulations produced 57.6 ± 4.2 excavation sites while the excavation model produced only 4.1 ± 2.0 , compared to an average of 2.8 ± 2.4 sites after 10 min of building in the experiments (figure 3a). Two-sided Kolmogorov–Smirnov tests found that, at every time evaluated, the results from the excavation model could not be distinguished from the empirical results (at the 0.01 level, and at all but one time at 0.05). The pheromone model was significantly different at every time.

There were 6.0 ± 1.4 termites working at the end of experiments, compared to 3.5 ± 3.0 in the excavation model. Because termites are drawn to excavation sites through aggregation (with spatial constraints limiting how many can occupy a site at once; see Discussion), the number of termites working slowly increases in the experimental results and excavation model (figure 3b). At 35 out of 55 times evaluated, two-sided Kolmogorov–Smirnov tests could not differentiate between the excavation model and the experimental results (at the 0.01 level, and at 23 out of 55 times at 0.05). Over more than the first 5 min (31 measurements), at only one time was the excavation model significantly different from the empirical data. The number of termites working in the pheromone model was much larger, with 19.2 ± 2.2 at the end of simulations. The pheromone model was significantly different from the empirical results at every time.

The average distance that termites moved soil pellets in our experiments was 1.5 ± 1.0 cm (where most pellets are carried short distances), compared with 0.4 ± 0.1 cm in the excavation model (exclusively short distances) and 3.8 ± 2.7 cm in the pheromone model (broad range of distances) (figure 3c). While neither simulation provides a close match to our experimental results, the distribution's shape for the excavation model better matches our experimental results, with a peak of transports at short distances of under 2 cm, while the pheromone model has a very broad distribution with no distinguishable peak.

4. Discussion

In this work we studied the de novo building activity of two species of *Macrotermes* on featureless soil and presented an analysis based on tracking individuals to identify factors that affect the early stages of construction. Our results suggest that the classic understanding of termite construction being driven by a putative cement pheromone neglects key mechanisms. Rather than a progression from random deposition across the soil surface to coordinated deposition at sites based on accumulation of cement pheromone, our findings highlight an initial disorganized phase with random excavations across the soil surface followed by coordinated excavation at sites with actively digging termites. Our results highlight the importance of aggregation—joining excavation sites at which more termites are currently working—as a key factor inducing individuals to join excavation sites, as opposed to possible chemical or physical cues associated with the soil. Thus, instead of a positive feedback loop for deposition through the build-up of cement pheromone, our observations indicate a positive feedback loop for excavation through the aggregation of workers.

The shared excavation sites provide a template for construction whereby excavated material is deposited on the verges and structures emerge. Deposition at the edge of excavation sites is reminiscent of behaviour in other termite species in tunnel excavation, where most workers deposit material as soon as space allows rather than carry it away from the tunnel mouth [26,27]. While other recent studies have reported the formation of quarries during building by social insects [16,28], they did not investigate the role of these quarries in organizing construction. These observations suggest that, in the first minutes of construction activity, excavation and deposition are closely linked as coupled behaviours rather than being two independent actions. Through simulations, we highlighted the ability of a process driven by aggregation at excavation sites to capture the empirical early building behaviour of termites more closely than a traditional model driven by a putative cement pheromone that triggers depositions, and demonstrated that it is possible for termites to generate accumulated clusters of depositions without the presence of a cement pheromone.

Other recent studies have similarly questioned the primacy of the cement pheromone mechanism as traditionally

understood [15–18], suggesting instead that the shape of the built structure is a stronger organizing cue [16] or that termites preferentially spend time on nest material but are not triggered by it to perform particular behaviours [17]. Although these studies also do not rule out the existence of a cement pheromone, they likewise demonstrate the importance of other cues in organizing *de novo* construction among termites.

While not previously considered in the context of collective construction, the aggregation mechanism that our analysis highlighted as an important organizing factor evokes the role of aggregation in facilitating many distributed behaviours among social insects. Ants and bees use aggregation to perform tasks such as recruiting foragers, protecting the colony and selecting nest sites [3,29,30]. Aggregation has also been extensively studied as a coordinating mechanism in cockroaches, which are members of the Order that contains termites [31,32].

Our observations and simulations also highlight a mechanism that limits the positive feedback of aggregation: excavating termites act as physical obstacles that limit other termites from joining an excavation site. Without this mechanism, all termites in the excavation model simulations quickly wind up working at the same site (electronic supplementary material, figure S3). With limited exceptions [33], previous simulation models typically do not incorporate collisions between agents, instead letting them pass freely through each other [1,10,12,13]. Crowding of this type was similarly found to be a major factor in the self-organizing of tunnel excavation in subterranean termites [15]. These examples suggest the importance of explicitly including termites' physical presence in future models.

This study suggests a number of important directions for future experimental work; these fall into two main themes. The first is to clarify the mechanisms underlying the phenomenology found by our statistical analysis. For instance, are there other identifiable factors that affect the transitions we have modelled as stochastic (e.g. a termite's decision to initiate a new excavation site or to stop excavating)? In particular, there are key open questions about what biological mechanisms underpin the observed aggregation behaviour. Our analysis indicated that termites are strongly influenced by the number of others at excavation sites they encounter, but did not explain how termites perceive this stimulus. In cockroaches, proposed cues for aggregation include the scent of other roaches [31] and a more humid microclimate that results from the respiration of groups [32]. Similar cues could affect the termite aggregation we observe. Indeed, one recent termite study suggested that the cue provided by recently deposited soil was akin to a colony odour, which influenced termites to spend time

nearby but did not otherwise affect their behaviour [17]. Notably, our results (analysis 2) indicated that cumulative site activity increases the likelihood that a termite will join an excavation site; this might indicate the presence of a chemical cue distinct from a cement pheromone (such as a colony odour) that attracts termites. These considerations suggest that termites may coordinate their behaviour in part through a chemically mediated mechanism, even if this chemical is not a cement pheromone as traditionally formulated.

The second main direction for future work is to extend this study of the building process to beyond the first minutes of construction. With our experimental set-up and tracking approach, the occlusion of termites by galleries and tunnels makes it impossible to track the activity and identity of individual insects beyond the first minutes of the construction process. In particular, our study did not determine a mechanism for the transition from the accumulation of soil along the edges of excavation sites to the creation of pillars and arches. Trials going beyond *de novo* construction may be able to better determine how termites build these coherent and functional structures. Simulations based on studies of insect behaviour—incorporating cues we intend to investigate such as moisture level, shapes of soil structures, and airflow—can be used to explore how construction might proceed over longer time scales. The long-term goal of this research is to understand how the insect behaviours identified through studies like this one give rise to the large-scale and complex mound architectures that ultimately emerge. Future efforts yielding more detailed information about how termites build and respond to stimuli will provide a richer understanding of how their behaviours facilitate self-organized construction and influence mound form.

Data accessibility. Data are available in the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.82h58> [34].

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