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Self-organized digging activity in ant colonies

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Abstract Many ant species adjust the volume of their underground nest to the colony size. We studied whether the regulation of the volume of excavated sand could result from an interplay between recruitment processes and ant density. Experiments were performed with different group sizes of workers in the ant *Messor sancta*. When presented with a thin homogeneous sand disk, these groups excavated networks of galleries in less than 3 days. The excavation dynamics were logistic shaped, which suggests the existence of a double feedback system: a positive one resulting in an initial exponential growth phase, and a negative one leading the dynamics to a saturation phase. The total volume of excavated sand was almost proportional to the number of workers. We then developed a model in which we incorporated the quantitative behavioral rules of the workers' digging activity. A positive feedback was introduced in the form of a recruitment process mediated by pheromones. The model predicts that the excavation dynamics should be logistic shaped and the excavation should almost stop despite the absence of any explicit negative feedback. Moreover, the model was able to reproduce the positive linear relationship between nest volume and colony size.

Keywords Self-organization · Digging behavior · Colony size · Nest size regulation · *Messor sancta*

Introduction

Most ant species excavate their nest in soil (Sudd 1969; Hölldobler and Wilson 1990). While there exists a great variability in their structure, a typical underground nest consists of the same basic units: a set of chambers interconnected by galleries (Délye 1971; Thomé 1972; Brian 1983; Tschinkel 1987, 1999a, 2004; Cerdan 1989; Rasse 1999; Cassill et al. 2002; Mikheyev and Tschinkel 2004). The simplest form of underground nest corresponds to one vertical shaft connecting one to several chambers (Tschinkel 2003). The complexity of ant-nest structure increases with the branching and interconnection of galleries. In some species such as *Formica pallidafulva* (Mikheyev and Tschinkel 2004), the nest has a tree-like shape. In its most complex forms, such as in *Solenopsis invicta*, some parts of the nest form a dense network (Cassill et al. 2002).

Several field studies have shown a consistent property of underground nests, namely that their volume is adjusted linearly or almost linearly to the size (population) of the colony (Tschinkel 1987, 1999b, 2004; Mikheyev and Tschinkel 2004). Intriguingly, in species that build large nests, much of the inner space appears to be unoccupied. Workers, brood and queen are mostly concentrated in the intermediate and lower parts of the nest, while the upper parts contain many chambers that are empty or sometimes filled with refuse material or seeds (Tschinkel 1999a, 2004). The linear relationship between nest volume and colony size also holds in laboratory conditions. This makes it possible to investigate both the excavation dynamics and the behaviors and interactions among ants in a controlled environment, and thus provide a better insight into the underlying growth and volume-regulation mechanisms (Chrétien 1996; Rasse 1999; Rasse and Deneubourg 2001).

One important question is to understand how the workers are able to coordinate and regulate their digging activity, especially when a large number of individuals work simultaneously on several distinct sites and only have access to local information. The use of chemical

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Table 1 Total volume of excavated sand in the model and in the experiments

	Ants	Disk diameter (cm)	Experiments			Model		
			Mean excavated volume (cm ³)	±SD	N	Mean excavated volume (cm ³)	±SD	N
Increasing density	50	20	25.35	±11.0	5	15.65	±3.1	40
	100	20	37.15	±9.2	5	37.36	±4.0	40
	200	20	65.27	±22.4	10	76.99	±3.7	40
Constant density	100	14	23.45	±6.0	10	30.22	±1.9	40
	450	30	107.39	±18.1	10	147.01	±6.5	40
	800	40	–	–	–	254.11	±11.5	40

communication in excavation behaviors has been suggested or shown in several species of ants (Wilson 1958; Wilson and Bossert 1963; Blum and Warter 1966; Imamura 1982; Blum 1996; Rasse 1999; Rasse and Deneubourg 2001). In this context, our main objective was to test whether the regulation of the volume of networks of galleries with group size can be a by-product of recruitment processes mediated by pheromones. Following this hypothesis, workers deposit a pheromone which will increase the probability of another ant digging in its vicinity. This pheromone evaporates and its concentration decreases with time, so that after a certain time, if no further excavation is performed at the site, digging behaviors will not any more be reinforced. Deneubourg and Franks (1995) have developed a model showing that the presence of such amplification mechanisms can adjust the excavation rate to the ant density.

In this study, we first performed an experiment to study the excavation of networks of galleries in the ant *Messor sancta* (Myrmicinae). We analyzed concurrently the digging activity at the individual and collective level in a two-dimensional standardized set-up. At the collective level, we quantified the growth dynamics of the networks of galleries built by groups of a variable number of ants. At the individual level, we quantified the behaviors involved in the digging activity and we estimated the probabilities associated with these behaviors. All quantified parameters were then incorporated into an individual-based model into which a recruitment process by chemical communication was introduced. The model's predictions confirmed that the excavated volume is a linear function of the number of ants.

Methods

Colonies and experimental set-up

We used three colonies of *M. sancta* collected in southwestern France (Narbonne). All colonies were composed of adult workers (population range: 2,000–5,000) and brood. *M. sancta* is a Mediterranean granivorous ant that excavates large nests in sandy grounds. The nest is structured in two parts: a central zone connecting superficially to deep chambers by vertical tunnels, the deepest chambers reaching several meters depth, and a peripheral zone that includes a large horizontal network of tunnels interconnecting several chambers filled with seeds or refuse material (Cerdan 1989).

The general experimental set-up consisted of a sand disk 5 mm in height. We used brusselian sand (a yellow sand of a very fine and homogeneous granularity) that was poured in a mold and moistened by spraying water (25 ml). The mold was then removed and the sand disk covered by a glass plate (25×25 cm). To prevent ants from escaping, an arena (∅=50 cm) with a wall coated with Fluon GP2 was placed around the sand disk. Each experiment began with the random dispersal of the ants around the disk.

In the collective-level experiments, the set-up was videotaped from above with a high-resolution digital camera (SONY DCR-VX1000E) for 3 days in time-lapse mode (2 s every 20 min). At the end of each experiment, the excavated sand was collected, dried for 1 week at room temperature and weighed.

To study the dynamics of the excavation, we developed an image analysis software with Aphelion (<http://www.adcis.net/>) to estimate every 20 min the volume of excavated sand. The software was calibrated by comparing the volume measured by image analysis with the volume of excavated sand collected at the end of the experiment.

Two different groups of experiments were performed in order to study the impact of group size on the digging activity and the resulting volume of excavated sand (Table 1). In a first group of experiments, hereafter called increasing density condition, we studied the influence of increasing group size on digging activity in a disk of sand 20 cm in diameter. Three group sizes were tested with 50 ($N=5$), 100 ($N=5$) and 200 ants ($N=10$).

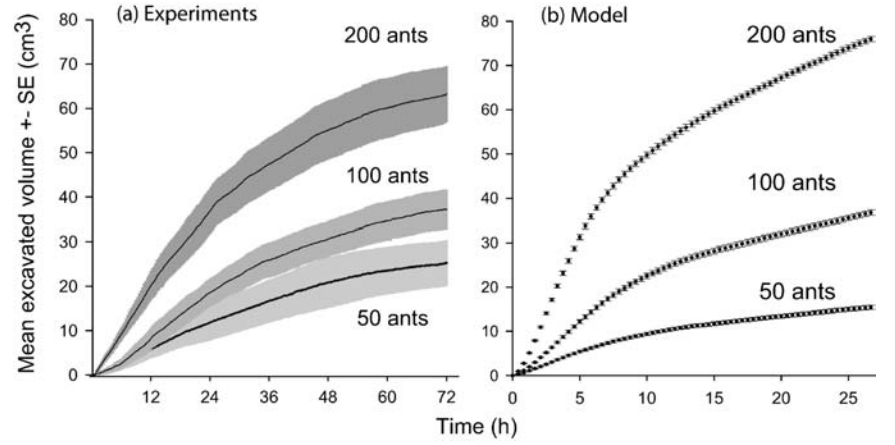
In a second group of experiments, hereafter called constant density condition, we kept constant the ratio between the number of ants and the surface of the sand disk. The original ratio was based on the value obtained with 200 ants and a disk 20 cm in diameter. We made a first set of experiments with 100 ants and a disk 14 cm in diameter ($N=10$), and a second one with 450 ants and a disk 30 cm in diameter ($N=10$). We were not able to use larger groups of ants due to the space limitation in the experimental set-up. In the constant ratio condition, we only measured the total amount of excavated sand.

We performed a separate set of experiments in order to analyze the individual behaviors. In these experiments, an artificial gallery was created in the sand disk by adding a plastic rod (10 cm long and 3 mm wide) perpendicularly to the edge of the mold. A group of 100 ants was placed in the arena and each experiment was videotaped for 1 h.

Statistical analysis

All analyses were conducted with SPSS 11.0 for Windows. Normality was tested with the Kolmogorov-Smirnov one-sample test, and homoscedasticity with a Levene test. To test the relation between the total excavated volume (v) and the number of ants (A), we performed linear regression tests on the log-log transformations ($\log v \approx \beta \log A$). The slope (β) of the fitted line allows us to estimate the value of the exponent in a power law. If this exponent value is equal to 1, the relation between the two quantities is linear.

Fig. 1 Mean dynamics of the volume of excavated sand by a group of 50, 100 and 200 ants **a** in the experiments, and **b** in the model. Note the difference of temporal scale between the experiments and the model.



Results

Experimental results at the collective level

Excavation dynamics

In all the experiments, the excavation dynamics had a logistic shape (Fig. 1a) and can thus be divided into three distinct phases: (1) an exponential growth in which the excavation rate progressively increases; (2) this amplification phase is followed by a short linear phase during which the excavation rate reaches its maximum value; (3) finally, a saturation phase in which the excavation rate progressively decreases to zero (see also Fig. 2a). This type of kinetics can be described with a classical Verhulst logistic model:

$$\frac{dv}{dt} = \alpha v \left(1 - \frac{v}{v_s} \right) \quad (1)$$

where α is a constant. Equation 1 corresponds to a double feedback process: a positive feedback corresponding to the term αv and a negative feedback corresponding to the term $1 - \frac{v}{v_s}$. The solution of this differential equation is:

$$v(t) = \frac{v_s}{1 + \left(\frac{v_s}{v_0} - 1 \right) \cdot e^{-\alpha t}} \quad (2)$$

where v_0 is an initial non-zero volume. This relationship can be written in a linear form as follows:

$$\text{Ln} \left(\frac{(v_s/v(t)) - 1}{(v_s/v_0) - 1} \right) = -\alpha t \quad (3)$$

Equation 3 was tested by a linear regression performed on each experiment; the initial volume v_0 was fixed to 1% of the mean total volume v_s measured in the 5 experiments performed with 100 ants. This yields a value $v_0 = 0.375 \text{ cm}^3$. This logistic model provided a good description of all excavation dynamics ($R^2 > 0.9$ in all cases).

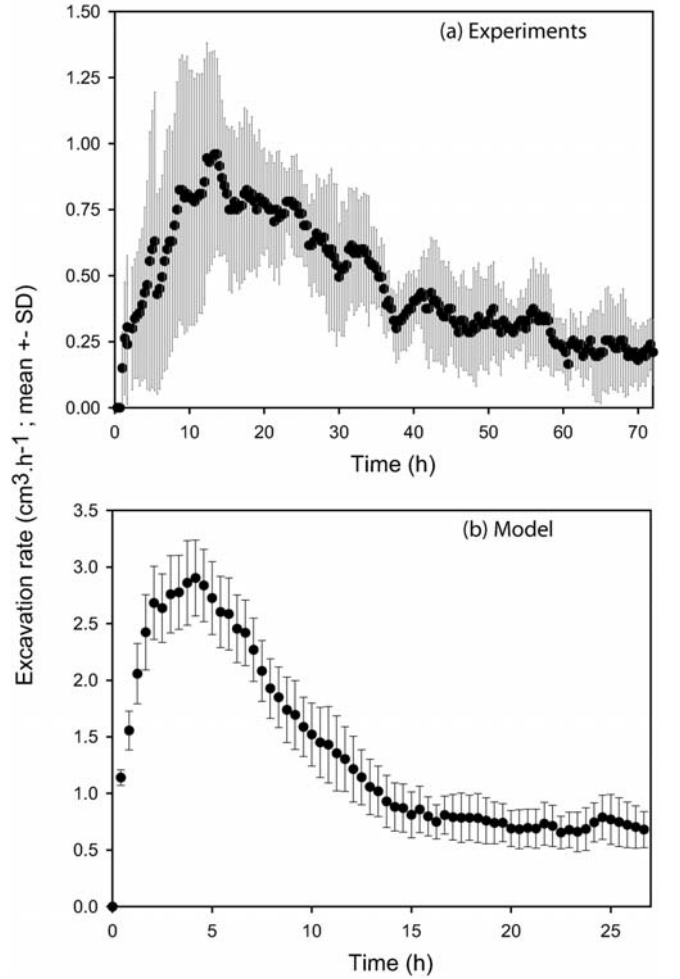


Fig. 2 Evolution of the mean rate of excavation with time **a** in the experiments, and **b** in the model with a group of 100 ants. Note the difference of temporal scale between the experiments and the model.

Relation between the volume of excavated sand and group size

The overall relation between the total volume excavated after 3 days and the number of ants when pooling the

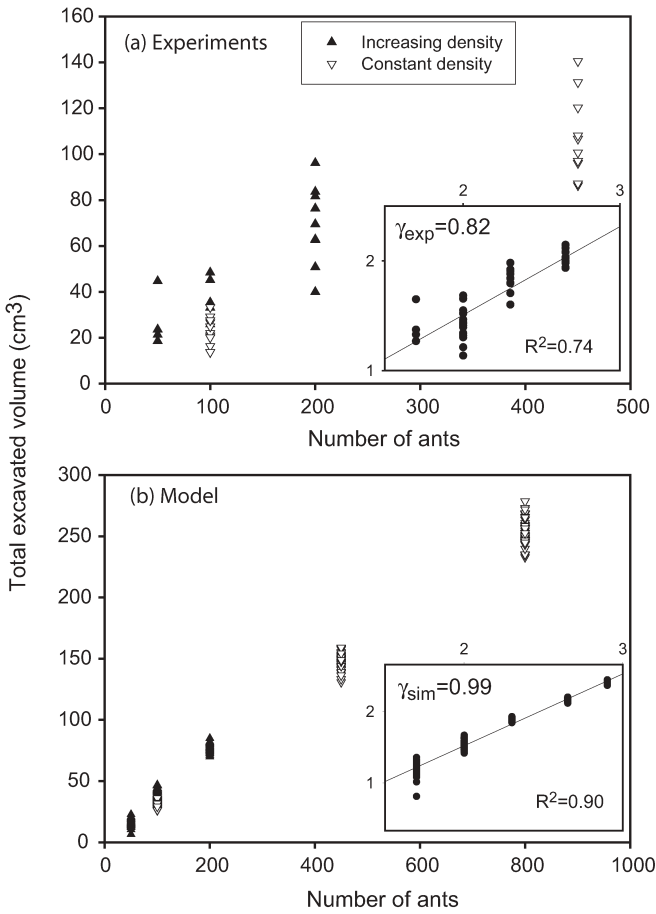


Fig. 3 Relation between the total volume of excavated sand (V_s) and the number of ants (A) in the experiments (a) and in the model (b). The insets show the log-log transformation and the linear regression fitting applied to all points. γ represents the slope value in the linear regression and corresponds to the power-law exponent in the relation $V_s = A^\gamma$.

results from all experiments was a power-law with exponent value $\beta=0.820$ (Fig. 3a; $R^2=0.74$; $N=40$; test against slope value $\beta=1$: $t=2.58$; $df=38$; $P=0.014$). This result shows that the total volume of the tunneling network built by ants is adjusted almost linearly to the size of the colony but with a tendency to grow slightly more slowly than the number of individuals.

However, there was also a significant effect of the size of the sand disk on the total excavated volume when we compared the two experimental groups with 100 ants (Table 1; Mann-Whitney test: $U=61$; $P<0.001$).

General description of the model

We developed a spatially explicit individual-based model in a discrete 2D square-lattice. The environment comprises four classes of objects: ants, ground, unexcavated and excavated sand. In the model, each ant can be in one of the following three states: free state, digging state, or transporting state. Ants can change from their present

state to another as a function of the environment encountered (see Fig. 4 and Appendix for details). They can start digging when they meet unexcavated sand, in which case they move into the digging state. An ant can be in the transporting state either when she has just finished digging, or when she encounters an excavated sand pellet on the ground and picks it up. The ant can then leave this state and come back to the free state by dropping its pellet.

Trail-laying and digging pheromones

Two kinds of pheromone were introduced into the model: a trail pheromone that influences ant displacement, and a digging pheromone, laid at the digging site, that controls the probability for an ant to dig.

Trail recruitment. An ant that is in the transporting state lays down a pheromone trail at each time step:

$$Q_t = Q_{t_0} - (F \times t) \quad (4)$$

where Q_t is the number of pheromone units laid down, Q_{t_0} the initial amount of pheromone laid by the ant, t the number of cycles elapsed since the transporting state began, and F the strength of the pheromone gradient. The attraction of ants by trail pheromone during their displacement is implemented by adding the amount of pheromone in the movement matrix Md (see appendix for details).

Signals and environmental cues triggering digging behavior. When an ant establishes a contact with the sand disk at a place where there is no pheromone, she can spontaneously start to dig with two different probabilities, f_s^a and f_s^h , depending on whether there is a depression (anfractuosity) in the sand wall (f_s^a), or not (f_s^h , which corresponds to a homogeneous straight sand wall). Several species of ants have been reported to be strongly stimulated to dig anfractuositities (Sudd 1970a, 1970b). To determine the presence of a depression in the sand, the ant “computes” the proportion of cells occupied by sand in 15 cells in the front and side directions of her surroundings (Fig. 4a). If this proportion is higher than 73.3% (more than 11 occupied cells), then the environment is considered to contain a depression.

When an ant is located at a place marked with digging pheromone, the ant starts to dig with a probability given by the following sigmoid response function:

$$f_p = X^2 / (X^2 + K^2) \quad (5)$$

where X is the amount of pheromone and K a threshold constant. Again, for an equivalent quantity of pheromone, an ant will be more stimulated to dig in the presence of a depression than in its absence: we fixed a value of K in the presence of a depression (K_a), and a higher value in its absence (K_h). In any case, each time an ant performs a digging behavior, she lays a fixed amount of digging

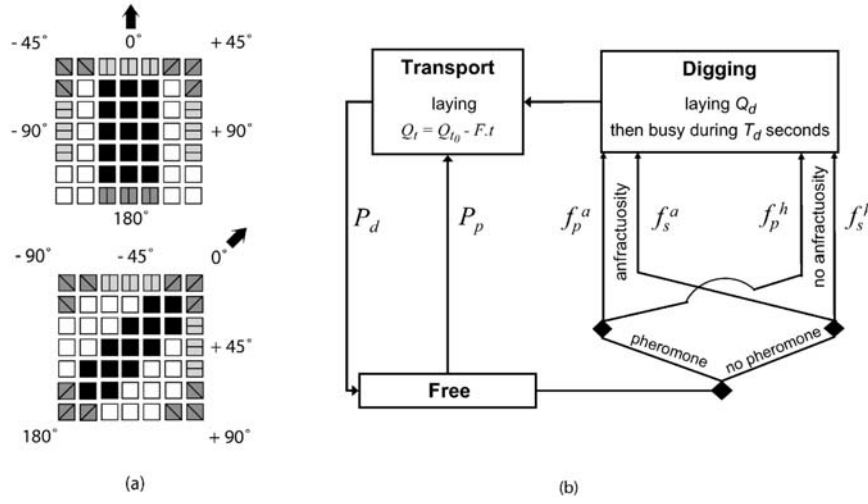


Fig. 4 Representation of an ant and its perception in the model (a) and flow chart (b) of the model. **a** The representation, in the model, of an ant oriented towards the north (upper part of the figure) and the northeast (lower part of the figure). *Black squares* represent the cells occupied by the body of ant. *Gray barred squares* represent the cells perceived by an ant in the six directions (0° , $\pm 45^\circ$, $\pm 90^\circ$ and 180°) in which she can move. Each direction is composed of

three cells that are represented by squares of the same color and same direction for the bars. When an ant has to determine whether she is in the presence of a depression in the sand wall, she counts the number of cells occupied by sand in 15 cells corresponding to all the directions except 180° (0° , $\pm 45^\circ$, $\pm 90^\circ$). **b** The three possible states for an ant and the probabilities to change from one state to another (see the text for full description).

Table 2 Parameters of the model (see text for description). The first part of the table gives the values of the probabilities to perform actions, calculated from the experiments. The second part gives the parameters describing the chemical physics of pheromones, which were not quantified in the experiments but estimated from previous works (X represents the quantity of digging pheromone)

Model parameters	Value	Origin	
T_d	Time required to dig one pellet	42.04 s	Experiments
P_d	Probability to drop a pellet	0.188 s^{-1}	
P_p	Probability to pick up a pellet	0.102/contact	
f_s	Probability to dig spontaneously		
	$-f_s^a$: in presence of a depression	0.054/contact	
	$-f_s^h$: in absence of a depression	$2.83 \cdot 10^{-2} \text{ s}^{-1}$	
f_p	Probability to dig in presence of pheromones*	$f_p = X^2 / (X^2 + K^2)$	Estimation
	$-f_p^a$: in presence of a depression	$K_a = 200$	
	$-f_p^h$: in absence of a depression	$K_h = 3500$	
Q_d	Quantity of digging pheromone per deposit	100 units	
$Q_{t(0)}$	Initial quantity of trail pheromone laid down	2000 units	
F	Gradient strength of pheromone trail	5	
μ_t	Half-life of the trail pheromone	40 min	
D_t	Diffusion coefficient of the trail pheromone	$3.22 \cdot 10^{-7} \text{ cm}^2 \text{ s}^{-1}$	
μ_d	Half-life of the digging pheromone	20 min	
D_d	Diffusion coefficient of the digging pheromone	$3.22 \cdot 10^{-7} \text{ cm}^2 \text{ s}^{-1}$	

pheromone on the cell where she is located and on one cell in front of her.

At the end of each time step, both pheromones are submitted to an evaporation and diffusion process (see appendix for details).

Statistical quantification of individual behaviors and model parameters

All parameters of the model were estimated by experimental measures (see also Table 2), except those describing the pheromones.

Ant velocity, digging time and weight of a sand pellet. The mean velocity of ants was estimated by tracking workers moving outside the sand disk and in the absence of any

obstacles (dividing for each ant total path length by total time of displacement). The distribution of displacement speed was Gaussian with a mean value of $S=15.05 \text{ mm/s}$ ($\pm 4.38 \text{ SD}$; KS test: $N=100$, $Z=1.14$, $P=0.149$).

From the video recording of events inside the gallery, we selected a random number of ants and we measured the time a worker spent digging a sand pellet. The distribution of digging times was Gaussian with a mean value of $T_d=42.04 \text{ s}$ ($\pm 24.79 \text{ SD}$; KS test: $N=65$, $Z=0.749$, $P=0.628$).

To determine the approximate weight of a sand pellet, we collected the excavated sand pellets and the resulting total amount of sand was dried and weighed. The estimated weight of a pellet was $W_p=1.69 \text{ mg}$ ($N=942$).

To scale the model to the experiments, the distance between two lattice cells was fixed to 0.8 mm and the time scale to $1/20 \text{ s}$ per cycle. Ants move on this grid with

a constant speed equal to the mean speed observed in experiments. The diameter of the sand disk was thus set to 250 cells for a 20-cm diameter disk. Since the thickness of the sand disk is not represented in the model, each cell representing the sand disk can be dug only once, letting ants excavate the whole sand disk after 54,323 digging acts. Therefore, the weight of a sand pellet in the model is 4.23 mg, which is 2.55 times higher than in the experiments. This mismatch between the experiments and the model may lead to differences in the temporal scale of the dynamics.

Probabilities to perform actions. The probabilities for an ant to drop a pellet of sand (P_d), to dig spontaneously (f_s^h) and to leave the edge of the sand disk (P_l) were estimated by analyzing the survival curves of these behaviors. An exponential decay in the survival curve indicates a constant probability per unit of time to perform the action. This constant probability can then be estimated by the slope of a linear regression performed on the semi-logarithmic representation of the data.

To estimate the probability to dig spontaneously in the absence of a depression in the sand wall (f_s^h), we made independent observations of randomly chosen ants ($N=94$) and we measured the time elapsed between the moment an ant made a contact with the edge of the sand disk and the moment she started to dig. This observation was limited to the first 15 min of the experiments at sites where no other ants had previously dug. The survival curve was exponential ($R^2=0.98$) and the estimated probability was $f_s^h=2.83 \cdot 10^{-2} \text{ s}^{-1}$.

To estimate the probability for an ant to spontaneously drop the pellet she carries (P_d), we made independent observations of haphazardly chosen ants ($N=2,077$) that were carrying a sand pellet and we measured the time interval between the end of digging and the spontaneous dropping of the pellet. The survival curve was exponential ($R^2=0.97$) and the estimated probability to drop a pellet was $P_d=0.188 \text{ s}^{-1}$.

To estimate the probability for an ant (P_l) to leave the edge of the sand disk she is following, we made independent observations of randomly chosen ants ($N=94$) and measured the duration of contact with the sand disk before the ant left the edge of the disk and moved away. This gives an estimation of the thigmotactic effect of the edge of the sand disk on ant movements. The survival curve was exponential ($R^2=0.94$) and the estimated probability was $P_l=1.76 \cdot 10^{-2} \text{ s}^{-1}$.

To estimate the probability P_p to pick a sand pellet, sand pellets were observed from the moment they were dropped by ants in the gallery until they were picked up by an ant. For each pellet, the number of ants passing over it until it was picked up was counted, which yielded a mean value of 9.76 (± 10 SD; $N=13$). The probability P_p was approximated as the inverse value, $P_p=0.102$.

The probability to dig spontaneously a depression in the sand wall (f_s^a) was estimated by recording the proportion of ants that started to dig at the dead-end of the artificial gallery. The proportion of ants that dug after

having entered the gallery was $f_s^a=0.054$ (6 events over 111 observed ants).

Comparison of the model predictions with the experimental results

All experimental situations were reproduced in the model (Table 1). The simulations were first run with 100 ants and a 20-cm-diameter disk to tune the pheromone parameters and test the ability to reproduce the growth dynamics observed in the experiments. In the constant-density condition, an additional set was run with 800 ants and a 40-cm-diameter disk.

Growth dynamics with 100 ants

The volume of excavated sand was recorded every hour. A phase of low excavation rate was reached after 27 h, a time past which the variation of this rate was never higher than $0.1 \text{ cm}^3/\text{h}$. Thus, all simulations were stopped at 27 h instead of the 72 h needed to reach a saturation phase in the experiments.

The model successfully reproduced the logistic shape of the excavation dynamics (Fig. 1b) and the evolution of the excavation rate with time (Fig. 2b). However, the results of the model and the experiments differed with respect to the time scale of the excavation dynamics: the mean maximal rate in the model was 3.01 times higher than in the experiments (simulations: $3.63 \text{ cm}^3/\text{h} \pm 0.6$ SD; experiments: $1.18 \text{ cm}^3/\text{h} \pm 0.3$ SD). The mean final excavation rate in simulations was not null but very low ($0.749 \text{ cm}^3/\text{h} \pm 0.4$ SD). It was 3.60 times higher than in the experiments ($0.21 \text{ cm}^3/\text{h} \pm 0.1$ SD). The ratio between the mean maximal rate and mean final rate was 4.84, which was similar to that observed in the experiments (5.60). We can therefore consider that the digging activity in the simulations has reached a saturation phase in a similar way as in the experiments. The logistic model (equation 3) provided a good description of all excavation dynamics ($R^2 > 0.81$ in all simulations). Comparisons were made for the mean total volume of excavated sand reached at the saturation phase in the model and the experiments for the same condition. There was no significant difference between the groups (Table 1; $T=-0.002$; $P=0.99$).

Growth dynamics in the increasing density condition

Dynamics were logistic in all simulations (Fig. 1b) whatever the conditions. The logistic model (equation 3) provided a good description of all excavation dynamics ($R^2 > 0.79$ in all simulations).

The same temporal scale bias as in simulations with 100 ants was observed. The final excavation rate increased significantly with the number of ants (Kruskal-Wallis test: $\chi^2=77.9$; $df=2$; $P<0.001$), following a linear

relationship (linear regression through the origin: $R^2=0.82$; $b=5.89 \cdot 10^{-3}$; $t=23.6$; $P<0.001$). This suggests that the last part of the growth dynamics corresponds to the occurrence of isolated spontaneous digging acts. As observed in the condition with 100 ants, the final rate was still around 3 times lower than the maximal rate. Therefore, the excavation dynamics still reached a saturation phase.

Relation between the volume of the tunneling network and group size

The overall relation between the volume and group size was a power-law with exponent $\beta=0.99$ ($R^2=0.90$; $N=280$; test against slope value $\beta=1$: $t=0.48$; $df=268$; $P=0.63$). Thus, in the simulations, the excavated volume was linearly adjusted to the number of ants.

The comparison between the 2 conditions involving 100 ants (20-cm-diameter and 14-cm-diameter disks) shows that varying the surface of available sand did affect significantly the mean total volume of excavated sand, similar to what was observed in experiments (Table 1; Mann-Whitney U -test: $U=61$; $P<0.001$).

Discussion

How are thousands of workers in an ant colony able to coordinate their activity while digging a complex network of interconnected galleries? The limited cognitive abilities of ants, their local perception of the environment and the dispersion of workers over many distant places prevent the colony from using direct communication or centralized control to coordinate its collective activity. Our study shows that the adjustment of the volume of a tunneling network to colony size may be a by-product of a recruitment process.

In the experiments, the evolution of the amount of excavated sand with time was logistic. Such growth dynamics are a signature of amplifications at the origin of self-organized activities (Bonabeau et al. 1997; Camazine et al. 2001). It suggests that amplification behaviors or recruitment processes are involved in this activity. When the number of ants varied, the total excavated volume was adjusted in an almost linear way, which confirms that this is a common feature of several species (Tschinkel 1987, 1999b; Chrétien 1996; Rasse 1999; Rasse and Deneubourg 2001; Mikheyev and Tschinkel 2004).

In this paper, we have developed an individual-based model to test the hypothesis that the properties of recruitment processes can be sufficient to induce an adjustment of the excavated volume to the size of the colony. In this model, the excavation dynamics were logistic and ended with a saturation phase at volumes that were similar to those observed in the experiments. However the temporal scale on which the phenomenon took place was much shorter, and a weak residual activity was observed at the end of the simulations. These differences were not

surprising considering the scale bias introduced by the value of the sand-pellet weight used in the model. The existence of a residual final digging activity is not surprising either, since in the model, all ants remain active throughout the simulation. Therefore, we can expect that at any time some ants will start to dig spontaneously (with the associated probabilities P_s^a and P_s^h) even if no recruitment processes take place, conferring to the dynamics a final phase of weak linear growth. In experiments, the absence of any residual activity could be favored by the competition between digging and aggregation behaviors. Other mechanisms, such as exhaustion of workers, could also strengthen the termination of digging activity at the end of the experiments.

In the model, the relation between the total excavated volume and the number of ants was best described by a linear relation, while in the experiments, the volume scaled with the number of ants with an exponent slightly lower than 1. This difference could result from the presence of other feedbacks in competition with the recruitment to digging sites: a potential mechanism could be the aggregation of ants (Deneubourg et al. 2002; Jeanson et al. 2004), whose interplay with excavation behaviors has been shown in the ant *Lasius niger* (Rasse 1999; Rasse and Deneubourg 2001). Another factor affecting the total volume of the network is the total initial space available to dig. The comparison between the 2 experiments involving 100 ants with 2 diameters, 14 cm and 20 cm, indicates that a smaller sand disk leads to a smaller total excavated volume. This effect was observed both in experiments and simulations and could result from the fact that tunnels propagate differently in sand disks of different sizes. Our hypothesis is that collisions between tunnels might be more frequent in a smaller sand disk. Thus, tunnels would tend to extend over shorter distances before colliding and new tunnels would be initiated more often. This effect would slow down the digging dynamics, thus resulting in a smaller excavated volume.

The model clearly shows that a regulation of the network volume as a function of the number of individuals can take place in the absence of a direct perception or measure of the excavated volume by ants. These results suggest that local amplification processes alone are sufficient to give rise to a double feedback system. (1) Positive feedbacks rapidly amplify the spontaneous acts of excavation that first occur randomly and in a disorganized way all around the sand disk. Among these initiation sites, some will involve several individuals so that recruitment will start. The system thus behaves in an autocatalytic way, leading the growth dynamics to its early phase of exponential growth. (2) Negative feedbacks progressively decrease the digging rate and lead to its termination when the volume of excavated sand reaches a critical value that was found to be proportional to the number of ants. As there is no explicit negative feedback implemented in the model, this effect should result from a decrease of the efficiency of the recruitment process when the ant density becomes too low (Deneubourg and Franks 1995). At the beginning of the simu-

lation, there is a high density of ants at the periphery of the sand disk, so that a recruitment process can easily take place. As the network grows, ants are more and more dispersed in space, and the probability for an ant to meet a site that another ant has recently dug before the pheromone has vanished completely becomes lower and lower. Finally, when the density of ants falls below a critical value, no recruitment can take place, because the time elapsed between the visits of two different ants at the same digging site becomes too important with respect to the half-life of the pheromones.

These results do not mean that recruitment is the only mechanism used by ants to adapt their nest volume. However, these results show that if pheromones are used in digging activity, the resulting amplification processes induce collective-level properties that are sufficient to account for the regulation of nest volume with colony size.

A deeper exploration of the model properties may provide important insights about the link between the excavation patterns and variations in the different model parameters reflecting differences between species or environments. One prediction of the model is that the half-life of the pheromones should have a crucial influence on the density at which the excavation activity stops. There exist strong variations of trail pheromone half-life between ant species (Edelstein-Keshet et al. 1995). Similar variations in the case of digging pheromones may result in vertical shifts in the linear relation between $\log(\text{number of ants})$ and $\log(\text{excavated volume})$, and thus in interspecific differences in the global density of ants in the nest. Furthermore, there should exist a critical density under which the recruitment process is unable to start, which may be studied both in the model and in experiments. Thus, we predict that very small groups in which the initial ant density would be below this critical density should not exhibit the typical features of a recruitment process such as logistic dynamics of excavation.

Variations in the environment, such as differences in the soil composition, may affect the time required to dig a sand pellet (T_d). Strong differences in T_d may in turn slow down the recruitment process, thus increasing the critical density and resulting in a smaller total excavated volume.

In our model and experiments, we worked with a fixed number of workers. In natural conditions, the number of workers in a colony is not fixed but constantly growing, and nest excavation is not a punctual event but rather the result of a long-term expansion. Deneubourg and Franks (1995) have shown in their model that a recruitment process can non-trivially produce different types of dynamics when the number of workers is regularly increased: the excavated volume can grow monotonously, and be constantly adjusted to the group size increase or occur by intense bursts of growth, separated by periods during which the group size increase does not lead to excavation. Given the recruitment process implemented in our model, such properties should also be observed for dynamically increasing group sizes.

Finally, we focused here on the volume, which is an important characteristic of ant nests but not the only one. Preliminary results show that varying the model parameters, such as the probability to dig spontaneously, can lead to completely different patterns, ranging from networks of growing galleries to amorphous large excavation fronts. Indeed, another key issue is to understand how the morphological characteristics of the network structure of the nest emerge from the local actions of ants.

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Appendix: description of the model implementation

At the beginning of a simulation, ants are randomly placed on the surface around the sand disk. All ants start in the free state. During a cycle, each ant is randomly chosen and performs a single action per time step.

Digging and carrying states

If an ant decides to dig, she comes into the digging state for T_d time steps; during this period the ant will not perform any other action. When this period of time ends, the ant enters into the transporting state. There exists another way for an ant to come into this state: each time an ant in a free state comes into contact with a pellet, she can pick it up with a constant probability P_p . When an ant is transporting a pellet, she has a constant probability P_d to spontaneously drop the pellet she carries and then enters back into the free state (Fig. 4b).

Ant movements

At the end of a simulation cycle, each ant that has not performed an action (digging, picking or dropping a sand pellet) moves randomly over a distance of one cell, in one of the six possible directions (0° , $+/-45^\circ$, $+/-90^\circ$ and 180° ; see also Fig. 4a) according to a weighted matrix (Md) that favors front directions. The weights applied to each direction are the following: 100 for 0° , 46 for $+/-45^\circ$, 6 for $+/-90^\circ$, and 1 for 180° .

The thigmotactic behavior of ants is implemented by weighting the cells, in the matrix Md , that are adjacent to the direction blocked by sand so that the probability to leave the sand wall is equal to the experimental probability (P_l). The movement matrix Md is modified by trail pheromones by adding the pheromone units present in each direction.

An ant cannot move on a cell already occupied by two other individuals. The simultaneous occupation of one cell by two ants was allowed since, in the experiments, we observed that one ant would frequently start to walk over another one when tunnels were crowded. Finally, an ant cannot move on a cell that contains sand and her displacement is restricted by the outside arena.

Evaporation and diffusion of pheromones

At the end of a cycle, evaporation and diffusion processes occur and are applied separately on the two kinds of pheromone. Evaporation is expressed by the following function:

$$Q_{t+1} = Q_t - (Q_t/\mu) \quad (\text{A1})$$

Q_{t+1} is the amount of pheromone in a cell at $t+1$ after it has lost a fraction of its previous amount Q_t ; μ is a constant representing the half-life of the pheromone.

Diffusion is implemented in the following way: a fraction of the amount of pheromone Q_c on a cell i is diffused to all neighboring cells n,i that have a smaller amount of pheromone $Q_{n,i}$ according to the function:

$$\begin{aligned} \text{If } Q_c > Q_{n,i} \text{ then } Q_c &= Q_c - (Q_c \times D) \text{ and } Q_{n,i} \\ &= Q_{n,i} + (Q_c \times D) \text{ for each neighbouring cell } i \end{aligned} \quad (\text{A2})$$

where D is a constant that represents the diffusion coefficient of the pheromone.

References

- Blum MS (1996) Semiochemical parsimony in the Arthropodia. *Annu Rev Entomol* 41:353–374
- Blum MS, Warter SL (1966) Chemical releasers of social behaviour. VII. The isolation of 2-heptanone from *Conomyrma pyramica* (Hymenoptera: Formicidae: Dolichoderinae) and its modus operandi as a releaser of alarm and digging behaviour. *Ann Entomol Soc Am* 59:774–779
- Bonabeau E, Theraulaz G, Deneubourg J-L, Aron S, Camazine S (1997) Self-organization in social insects. *TREE* 12:188–193
- Brian M (1983) Social insects : ecology and behavioural biology. Chapman & Hall, London
- Camazine S, Deneubourg JL, Franks N, Sneyd J, Theraulaz G, Bonabeau E (2001) Self organization in biological systems. Princeton University Press, Princeton
- Cassill D, Tschinkel WR, Vinson SB (2002) Nest complexity, group size and brood rearing in the fire ant, *Solenopsis invicta*. *Insectes Soc* 49:158–163
- Cerdan P (1989) Etude de la biologie, de l'écologie et du comportement des fourmis moissonneuses du genre *Messor* (Hymenoptera, Formicidae) en Crau. PhD thesis, Université de Provence, Aix-Marseille I
- Chrétien L (1996) Organisation spatiale du matériel provenant de l'excavation du nid chez *Messor barbarus* et des cadavres d'ouvrières chez *Lasius niger* (Hymenoptera : Formicidae). PhD thesis, Université Libre de Bruxelles, Brussels
- Délye G (1971) Observations sur le nid et le comportement constructeur de *Messor arenarius*. *Insectes Soc* 18:15–20
- Deneubourg JL, Franks NR (1995) Collective control without explicit coding : the case of communal nest excavation. *J Insect Behav* 4:417–432
- Deneubourg JL, Lioni A, Detrain C (2002) Dynamics of aggregation and emergence of cooperation. *Biol Bull* 202:262–267
- Edelstein-Keshet L, Watmough J, Ermentrout GB (1995) Trail following in ants: individual properties determine population behaviour. *Behav Ecol Sociobiol* 36:119–133
- Hölldobler B, Wilson EO (1990) The ants. Springer, Berlin Heidelberg New York
- Imamura S (1982) Social modifications of work efficiency in digging by the ant, *Formica yessensis* Forel. *J Fac Sci Hokkaido Univ Ser VI Zool* 23:128–142
- Jeanson R, Deneubourg J-L, Grimal A, Theraulaz G (2004) Modulation of individual behavior and collective decision-making during aggregation site selection by the ant *Messor barbarus*. *Behav Ecol Sociobiol* 55:388–394
- Mikheyev AS, Tschinkel WR (2004) Nest architecture of the ant *Formica pallidefulva*: structure, costs and rules of excavation. *Insectes Soc* 41:30–36
- Rasse P (1999) Etude sur la régulation de la taille et sur la structuration du nid souterrain de la fourmi *Lasius niger*. PhD thesis, Université Libre de Bruxelles, Brussels
- Rasse P, Deneubourg JL (2001) Dynamics of nest excavation and nest size regulation of *Lasius niger* (Hymenoptera: Formicidae). *J Insect Behav* 14:433–449
- Sudd JH (1969) The excavation of soil by ants. *Z Tierpsychol* 26:257–276
- Sudd JH (1970a) The response of isolated digging worker ants [*Formica lemmani* and *Lasius niger*] to tunnels. *Insectes Soc* 17:261–271
- Sudd JH (1970b) Specific patterns of excavation in isolated ants. *Insectes Soc* 17:253–260
- Thomé G (1972) Le nid et le comportement de construction de la fourmi *Messor ebeninus*, Forel (Hymenoptera, Formicoidea). *Insectes Soc* 19:95–103
- Tschinkel WR (1987) Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. *Insectes Soc* 34:143–164
- Tschinkel WR (1999a) Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*: distribution of workers, brood and seeds within the nest in relation to colony size and season. *Ecol Entomol* 24:222–237
- Tschinkel WR (1999b) Sociometry and sociogenesis of colony-level attributes of the Florida harvester ant (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 92:80–89
- Tschinkel WR (2003) Subterranean ant nests: trace fossils past and future? *Palaeogeogr Palaeoclimatol Palaeoecol* 192:321–333
- Tschinkel WR (2004) The nest architecture of the Florida harvester ant, *Pogonomyrmex badius*. *J Ins Sci* 4:21, available online. <http://www.insectscience.org/4.21>
- Wilson EO (1958) A chemical releaser of alarm and digging pheromone in the ant *Pogonomyrmex badius* (Latreille). *Psyche* 65:41–51
- Wilson EO, Bossert WH (1963) Chemical communication among animals. *Recent Prog Horm Res* 19:673–713