

Self-Organized Networks of Galleries in the *Ant Messor Sancta*

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Abstract. In this paper we describe an individual-based model to account for the growth and morphogenesis of networks of galleries in the ant *Messor sancta*. The activity of the individuals depends only on their local perception of the immediate surroundings. Coordination between ants arises from the modifications of the environment resulting from their activity: the removal of sand pellets and a pheromone trail-laying behaviour. We show that the growth of the networks results from a self-organized process that also allows the collective adaptation of the size and shape of the network to the size of the colony.

1 Introduction

Numerous animals that live in group or societies use or create networks. Among networks, those resulting from construction behaviour such as nest structures built by social insects are probably the most fascinating but also the least understood. Several species of ants build complex networks of underground tunnels that connect chambers [1-7]. Such structures are built without any blueprint or centralization processes [8]. Ants achieve such complex features using stigmergic processes [9], in which the modification of the environment that results from individuals' activity acts as a feedback on their behaviour. When the intensity of a building stimulus changes the probability for an individual to exhibit a specific behaviour, the resulting construction is a self-organized process [10]. Self-organization leads to the emergence of large-scale patterns from a homogenous environment through many local interactions among units at the lower level [11]. It thus allows the growth of complex structures without any centralization of information at the individual level. Self-organization has been shown to be involved in numerous collective behaviours in insect colonies [10,12,13] and also in vertebrates [14-16].

Several studies report that a constant relationship exists between nest size and population within a particular species in ants [17-20]; but little is known about mechanisms involved in achieving such adaptation. A first mechanism could be a direct triggering of the digging activity according to the perception of specific cues by individuals [21], such as a chemical signal whose concentration would be correlated

with the density of workers within the nest; however a recent study of the dynamics of nest excavation in *Lasius niger* [6,7] suggested that regulation of subterranean nest size could arise without such cues, from a combination of amplification processes and a tendency of individuals to aggregate themselves.

In this context, we studied the processes involved in the morphogenesis of galleries networks in the ant *Messor sancta* (Myrmicinae). It is a Mediterranean granivorous ant that digs large nests in sandy grounds and its colony size reaches several thousands of individuals. Nest structure is made of two parts: a central zone connecting superficial chambers to deep ones 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 used as seeds stocks.

The phenomenon was studied at two distinct levels: (1) at the collective level, we quantified the growth dynamics of the networks produced by 100 ants; (2) at the individual level, we quantified all the behaviours involved in the ants' activity. Finally, to understand the link between these two levels, we built a model including all the behavioural parameters drawn from experiments and we used it to study the adaptation of the resulting network for various colony sizes.

2 Experimental Result

2.1 Growth Dynamics

The general experimental set-up consisted in a sand disk of 20cm diameter and 5 mm height. It was prepared with a mould in which sand was deposited and humidified by 25 ml of sprayed water. The mould was removed, the disk covered by a glass (25 cm x 25cm) and the surface which ants had access to was restricted by a circular wall coated with fluon. 100 ants were collected from a colony and the experiment began with their random dispersal around the disk. A digital camera was placed over the arena. The duration of each experiment was 3 days, and 2 seconds of activity were recorded every 10 minutes. An image analysis software allowed us to quantify the volume of excavated sand (fig. 1).



Fig. 1. Example of tunneling pattern produced by 100 ants over 3 days. The pictures shown are the results of image analysis processes that allowed us to obtain binary images where the sand is represented by black pixels and the ground by white pixels.

Figure 2 shows the evolution of the volume of excavated sand as a function of time over 3 days in 5 experiments. In all experiments, the growth dynamics has a sigmoid

shape and can be divided in 3 phases: first, an exponential growth in which the excavation speed, nil at the beginning of experiment, progressively increases; this amplification phase is followed by a short linear phase during which the excavation speed reaches its maximum value; finally, a saturation phase in which the excavation speed decreases progressively to reach zero. This suggests two kinds of feedbacks: (1) a positive feedback when the volume V of excavated sand is far from a saturation volume, V_{max} (V/V_{max} is very small): the speed dV/dt grows proportionally with V . (2) a negative feedback when V becomes closer to V_{max} ($V/V_{max} \approx 1$): dV/dt decreases and reaches a null value. This kinetics can be formalized as follows:

$$dV/dt = aV [1 - (V/V_{max})] \tag{1}$$

where a is a constant. The solution of this differential equation is:

$$V(t) = V_{max} / [1 + ((V_{max} / V_0) - 1) \cdot e^{-at}] \tag{2}$$

where V_0 is a initial non-zero volume. This relationship can be easily written in a linear form as follows:

$$\text{Ln} [(V_{max}/V(t))-1] = \text{Ln} [(V_{max}/V_0) - 1] - at \tag{3}$$

Table 1 shows the results of the linear regression test for equation (3) in each experiment and the final size of the networks. Measures were made every 20 minutes, which represents a set of 217 data points per curve. V_{max} value was estimated as the volume excavated at the end of the experiment. In all cases r^2 values were always greater than 0.9 and the parameters for linear regression test were validated ($p < 0.001$).

These results show that growth dynamics is controlled by two kinds of feedbacks. Positive feedback could be the consequence of some recruitment processes, which will be confirmed later with the model. As regards negative feedback, when the saturation phase was reached, we always observed the formation of ants' aggregates. As a consequence, aggregation may be a first negative feedback involved in the saturation phase.

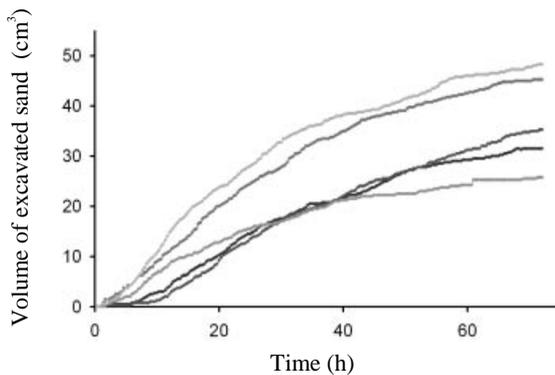


Fig. 2. Growth dynamics of networks with 100 ants over 3 days.

Table 1. Linear regression results for the logistic model (see text and equation 3 for details) and final volume and weight excavated after 3 days.

	r^2	a	Final volume (cm ³)	Final weight (g)
1	0.937	0.106 ± 0.002	33	49.04
2	0.929	0.11 ± 0.002	35.25	53.38
3	0.947	0.0986 ± 0.002	45	66.87
4	0.943	0.092 ± 0.002	25.75	38.27
5	0.923	0.0922 ± 0.002	48.25	71.7

2.2 Individual Behaviours

In this section, we describe all the individual behaviours involved in the digging activity of ants. We present the estimated mean values and probabilities to perform an action that were used in the model.

For the individual behaviour study, an artificial tunnel was created in the sand disk by adding a plastic shape 10 cm long and 3 mm wide. The number of ants was fixed to 100, and the recording time to 1 hour. The video recording was set to continuous mode.

Mean values. The distribution of walking speed was Gaussian with a mean value of 15.05 mm/s (N=100, SD=4.381, Z=1.139, p=0.149, Kolmogorov-Smirnov test). The distribution of digging time was Gaussian with a mean value of 42.04 s (N=65, SD=24.79, Z=0.7490, p=0.628, Kolmogorov-Smirnov test). The estimate weight of a pellet was 1.688 mg.

Probabilities to perform actions. Probabilities to perform actions were established from survival curves whenever it was possible. Given N_0 , the total number of individuals, N the number of individuals having not yet performed an action at time t, and λ the probability to perform the action, if λ is constant, then the evolution of the population N follows equation 4; λ can be estimated with a linear regression test on the logarithmic transformation of equation (4).

$$N = N_0 e^{-\lambda t} \quad (4)$$

$$\text{Ln}(N) = \text{Ln}(N_0) - \lambda t \quad (5)$$

Table 2 shows the experimental values for the probabilities to spontaneously dig the edge of the sand disc (f_s^h), to drop a pellet (P_d) and to leave the edge of the sand disk while following it (thigmotactic effect) (P_l). In each case equation (5) was tested and a linear regression validated with high r^2 values, which means that in each case the probability to perform the action is indeed constant over time and equal to the value of slope in the regression model.

Table 2. Results of the survival curves for three behaviours. r^2 values are indicated for linear regression test on equation (5) . The parameter λ represents the slope of the linear equation and corresponds to the probability to perform the action per second (see text for details).

Variable	r^2	Coefficient			
		λ	Std Err	T	p
To dig spontaneously (f_s^h)	0.985	$-2.83 \cdot 10^{-2}$	0.000	-54.76	0.00
To drop a pellet (P_d)	0.971	-0.188	0.001	-17.45	0.00
To leave the edge of sand disk (P_l)	0.944	$-1.76 \cdot 10^{-2}$	0.000	-24.95	0.00

The probability to dig spontaneously an anfractuosity (f_s^a) was estimated by the proportion of ants that dug after having penetrated in the artificial gallery (never dug before); its value was $f_s^a=0.054$ (6 ants over 111 observed). The dead-end of the tunnel represents a strong heterogeneity in the curvature of the sand in comparison with the rather straight sand walls in a tunnel or the edge of the sand disk. In this paper, we will use the term anfractuosity to refer to this kind of heterogeneity. Several species of ants are reported to be more strongly stimulated by anfractuositities [22] than by straight sand walls, and our results show that it is also the case in *Messor sancta*.

3 Model Description

The experimental analysis allowed us to quantify several parameters of the individual tunneling behaviour of ants. We developed a model entirely based on the experimental measures of individual behaviour, using a spatially-explicit individual-based simulation written in C++. In the model, ants move on a discrete 2D square-lattice preserving time and spatial scales of the experiments, with a distance of 0.8 mm between lattice cells and a time scale of 1/20 s per cycle. The environment includes 4 classes of objects: ants, ground, sand in the disk and excavated sand pellets.

3.1 Structure of the Model

Each ant can be in one of the following three internal states: free state, digging state, or transporting state. Ants can change from their present state to another as a function of the environment they meet according to the experimentally estimated probabilities.

At the beginning of the simulation, as in the experiments, ants are randomly distributed around the sand disk and are in the free state. During a cycle, each ant is randomly chosen and performs a single action one time and only one.

When an ant meets the sand disk, she can spontaneously start to dig, with two different probabilities, f_s^a and f_s^h , measured in the experiments, whether she is in presence of an anfractuosity in its immediate neighbourhood (f_s^a , high concavity in the

sand wall), or not (f_s^h , straight sand wall). When an ant enters into the digging state, she stays in this state for T_d time steps and no other action can be done. When this period of time ends, the ant enters into the transporting phase. There exists another way for an ant to enter into this phase: each time a free ant occupies a place where a pellet is present, 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 and return to the free state.

At the end of a cycle, each ant that has not performed an action (digging, picking or dropping a sand pellet) moves randomly to an adjacent cell, in one of the six possible directions (forward, back, 45° left or right and 90° left or right) according to a probability matrix (M_d) that favours front directions. The thigmotactic behaviour of ants is implemented by multiplying the weight of the cells adjacent to the direction blocked by sand in the matrix, so that the probability to leave the sand wall is equal to the experimental probability (P_l). Finally, an ant can move neither on a cell already occupied by two other individuals nor on a cell that contains sand and her displacement is restricted by an outside arena wall.

This basic algorithm that takes into account all the behavioural parameters that were measured in the experiments was not able to reproduce the emergence of tunnels and networks. The resulting digging dynamics was always linear until the ants have dug the whole sand disk. At this point, the main question was: how can the probabilities to dig sand evolve in order to produce networks of galleries? Several hypotheses that we won't present here, such as individual experience, have been tested, but only one additional mechanism, namely the use of trail-laying pheromones, was able to give rise to networks. The use of trail-laying pheromones is a widespread feature in ants and termites [10] and it has been shown to be involved in recruitment and digging behaviour in other ant species such as *Lasius niger* [6]. Trail-laying parameters are very hard to measure and they have been fixed by numerical exploration in the range of biological values already known from previous experiments performed on other species [6,23,24].

Two kinds of pheromone are used in the model: a trail-laying pheromone that influences ant displacement, and a digging pheromone laid at the digging site that controls the probability for an ant to dig a sand cell.

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

$$f_p = X^2 / (X^2 + K^2) \quad (6)$$

where X is the amount of pheromone and K a threshold constant. This class of response function provides a good approximation of the influence of pheromone on ant behaviour and it has been used in numerous works including collective recruitment and digging in ants [10,24,25]. In accordance with the experimentally measured probabilities to dig spontaneously, we determined one value of K , in presence of an anfractuosity (K_a) and a smaller value in absence of anfractuosity (K_b). In any case, each time an ant performs a digging behaviour, she will deposit a fixed amount of digging pheromone on the cell where she is located and on one cell forward according to the axis of her body.

When an ant enters the transporting phase, she will now lay down a trail pheromone at each cycle:

$$Q_t = Q_{t_0} - (F \times T) \tag{7}$$

where Q_t is the number of units of pheromone laid down, Q_{t_0} the initial amount of pheromone, T the number of cycles elapsed since the ant entered into the transporting phase and F the strength of the pheromone gradient. The attraction of ants by trail pheromone during their displacement is implemented by adding pheromone quantities in the matrix M_q .

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

$$Q_{t+1} = Q_t - (Q_t / \mu) \tag{8}$$

Q_{t+1} is the new amount of pheromone in a cell after it has lost a fraction of it 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 on a cell (Q_c) is diffused to each neighbouring cell that has a smaller amount of pheromone (Q_n) according to the function:

$$\text{If } Q_c > Q_{n,i} \text{ then } Q_c = Q_c - Q_c/D \text{ and } Q_{n,i} = Q_{n,i} + Q_c/D \tag{9}$$

for each neighbouring cell I

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

Figure 3 shows a graphical representation of the model and the values of all the parameters are given in table 3.

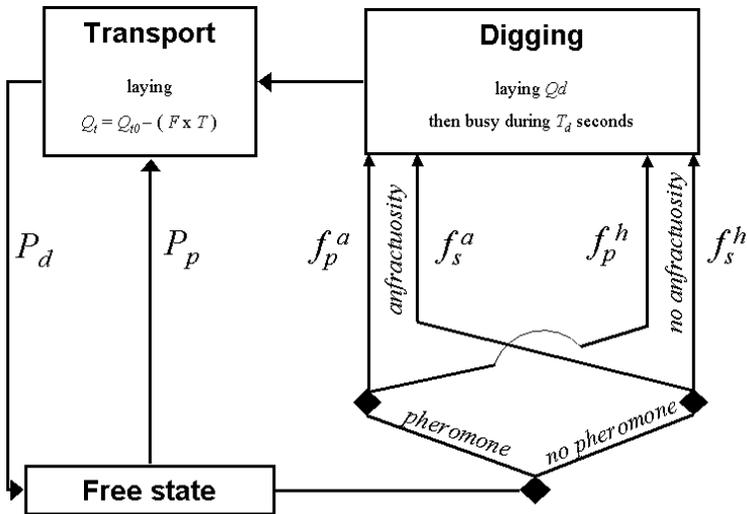


Fig. 3. Graphical representation of the model. The figure shows the three states possible for an ant and the probabilities to change from one to another (see the text for description)

Table 3. Parameters of the model.

Model parameters		Value	Origin
T_d	Time required to dig one pellet	40 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 anfractuosity	0.054 / contact	
	$-f_s^h$: in absence of anfractuosity	$2.83 \cdot 10^{-2} \text{ s}^{-1}$	
f_p	Probability to dig in presence of pheromones	$fp = X^2 / (X^2 + K^2)$	estimation
	$-f_p^a$: in presence of anfractuosity	$K_a = 200$	
	$-f_p^h$: in absence of anfractuosity	$K_h = 3500$	
Q_d	Quantity of digging pheromone per deposit	100 units	
$Q_{(t0)}$	Initial quantity of trail pheromone laid down	2000 units	
F	Gradient strength of pheromone trail	5	
μ_t	Half-life parameter of the trail pheromone	45 min	
D_t	Diffusion coefficient of trail pheromone	500 000	
μ_d	Half-life parameter of digging pheromone	20 min	
D_d	Diffusion coefficient of digging pheromone	500 000	

3.2 Results

40 simulations reproducing the experimental conditions described in section 2.1 were run with 100 ants, over a simulated time of 3 days. The volume of excavated sand was recorded every hour. Figure 4 shows an example of tunneling pattern obtained with the model with 100 ants over 3 days, and figure 5 shows 5 runs of the growth dynamics obtained in the same condition.

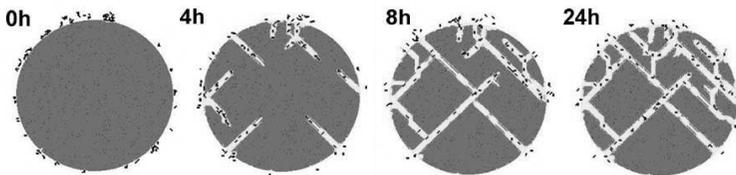


Fig. 4. Example of simulated tunneling pattern obtained with 100 ants.

The model succeeds in reproducing the logistic shape of the growth dynamics observed in the experiments, but the time needed to reach the saturation phase was three times shorter. This could be explained by two facts: first, the sand disk can be

dug completely in 54323 digging acts, with a sand pellet's weight of 4.298 mg, which is 2.546 times more than the experimentally measured mean weight (1.688 mg). Thus, in the model, ants excavate a volume of sand similar to the one obtained in experiments by performing around 3 times less digging acts; second, no aggregation processes were implemented in the model, so that all ants remained active during the simulation.

The linear regression described in section 2 was applied on the simulations results and the logistic model was always validated with high r^2 values (minimal r^2 value: 0.812). Comparisons were made for the mean final volume of excavated sand reached in the saturation phase in the model and the experiments for the same conditions. There was no significant difference between groups (model: $37.14 \pm 4.23 \text{ cm}^3$; experiments: $37.15 \pm 9.35 \text{ cm}^3$; $t=-0.002$; $p=0.998$, Student t test).

As in the experiments, the simulated dynamics appeared to be controlled by two kinds of feedbacks. A positive feedback resulting from the recruitment processes through trail and digging pheromones. Since there is no aggregation behaviour implemented in the model, the negative feedback may come from the fact that there exists some critical value of ant density in the network under which the amplification processes would fail to be efficient. At the beginning of the simulation, there is a high density of ants in the periphery of the sand disk, so that a recruitment process can take place. As the network grows, ants are more and more diluted in space, and the probability for an ant to meet a site recently dug and with sufficiently high pheromone

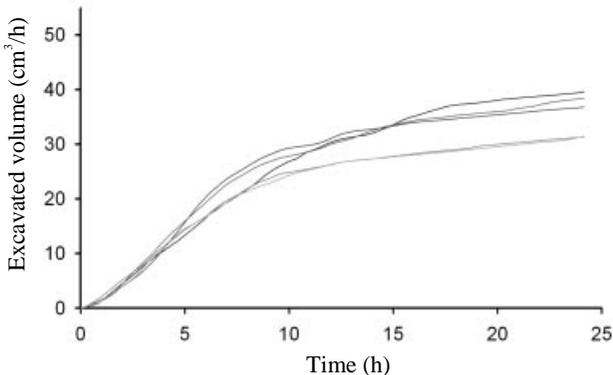


Fig. 5. Five examples of simulated growth dynamics obtained with 100 ants over the first 25 hours.

concentration becomes lower and lower. Finally, when the density of ants falls under a critical density, no recruitment can take place, since the mean time separating the visits of two different ants at the same digging site becomes too important with respect to the half-life of pheromones.

Such a mechanism of regulation of the digging activity could be a very efficient way to allow the colony to adapt the nest size to its population. If the digging activity stops when a certain density is reached, then we would observe a linear relationship between the number of ants and the total volume of excavated sand at the saturation phase.

3.3 The Influence of Colony Size

The model was used to assess the influence of the number of ants on the growth dynamics. 40 simulations were performed with 50 ants and 200 ants respectively over a simulated time of 3 days. Then, to test the predictive value of the model, we performed 5 corresponding experiments with 50 and 200 ants over 3 days.

Dynamics were logistic for all groups. The same linear regression procedure described in section 2.1 was applied to the dynamics and was in all cases validated by high r^2 values (minimal r^2 value: 0.79).

Figure 6a shows the mean volume of excavated sand as a function of the number of ants. A linear regression through origin was tested for the simulation results and validated with a high r^2 value ($r^2=0.993$; $b=0.379$; $t=133$; $p<0.001$). Thus, the model predicts that the total volume of the network at saturation phase follows a linear relationship with the population size. Indeed, this relationship was confirmed by the experiments (Figure 6b). The linear regression was validated with high r^2 values ($r^2=0.915$; $b=0.487$; $t=12.313$; $p<0.001$). These results show that there exists a regulation of the volume of the network according to the number of individuals. The model shows that this regulation arises in absence of any direct communication between ants; this results from a simple balance between recruitment processes and ants density. Moreover our model predicts that ants stop their activity when their mean density reaches 2.83 ± 0.64 ants/cm³. This was indeed confirmed by experiments in which the digging stopped at the same mean density value of 2.80 ± 1.15 ants/cm³.

4 Discussion

How can thousands of individuals in an ant colony coordinate their activity while digging a complex network of galleries and chambers? Ants limited cognitive abilities and their local perception of the environment as well as the dispersion of workers over many distant places prevent the colony using direct communication or centralized control to coordinate its collective activity. We have presented here a model of the growth of networks of galleries that exhibits adaptive properties. The size of the network is adapted to the size of the colony, even though each ant is not

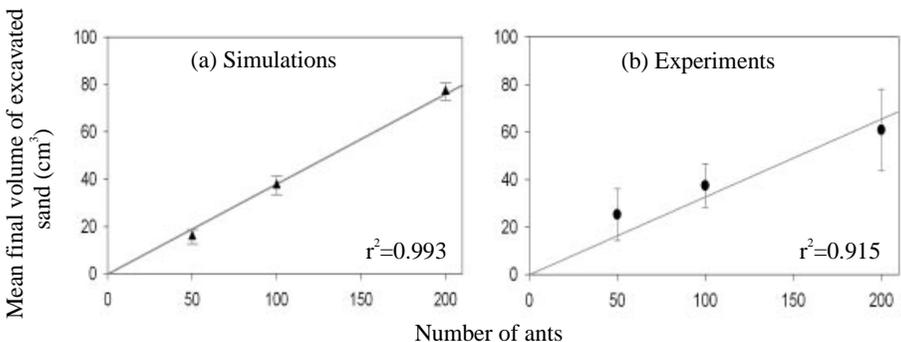


Fig. 6. Linear relationship between the final volume of excavated sand and the number of ants in the model (a) and in the experiments (b)

aware of the total number of ants in the nest. Each individual is an autonomous agent that has only a very local perception. Individuals use previous modifications in the environment by each ant as a feedback to coordinate their activity. The regulation of the network volume relies entirely on indirect communication mediated by the environment, mainly through the use of trail and digging pheromone combined with the density of ants that acts as an indirect cue. The collective regulation of the size of the galleries network is not explicitly programmed at the individual level and appeared to be an emergent property of the digging dynamics.

The study has been divided into three main steps. First, we performed an analysis at the global level through experiments with a constant population of 100 ants. We characterized the growth dynamics of the amount of excavated sand and showed that they are logistic. We then focused on the individual level and showed that several behaviours had a remarkably constant probability to occur. We finally used these experimentally measured parameters in the behavioural rules of the agents in an individual-based model. Introducing recruitment processes through pheromones, a common feature involved in several activities of ants, we showed that a group of ants is able to regulate their digging activity and stop it when a certain volume is reached, even if the individuals are still active and that nothing changed in their behavioural rules. This is consistent with the results on digging behaviour and tunnel construction in the ant *Lasius niger* [6], in which it has been shown that a volatile molecule was involved in the recruitment of ants towards a digging site.

When loaded with the experimental parameter values, the model not only leads to growth dynamics that reproduce the properties of galleries network formation, but also predicts how the growth is affected by the density of ants. We found that the final volume of excavated sand followed a linear relationship with the number of individuals. Experiments designed to test the model's predictions show that the predictions are indeed confirmed and the networks dynamics exhibit the same adaptive properties.

This coordination of digging activity in the ant *Messor sancta* emerges from a double feedback system:

- (1) Positive feedbacks rapidly amplify spontaneous acts of excavation that first occur randomly and in a disorganized way all around the sand disk. Among these isolated 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. As it is shown in the model, this recruitment phase could result from the use of marking at the digging site with a highly volatile component and from the use of pheromone trails leading the individuals to the digging sites.

- (2) Negative feedbacks progressively decrease the speed of digging and lead to its end when the volume of excavated sand reaches a critical value proportional to the number of ants. This mechanism of size adaptation of the network could result from a combination of aggregation processes and the decrease of ant density with time. This is consistent with the results of a previous study of nest size regulation in the ant *Lasius Niger* [6,7]. But the model shows that the decrease of ant's density alone could be sufficient for a colony to adapt the size of the network to the size of its population.

There exists a whole number of experimental evidence that shows that several other social phenomena such as aggregation behaviour or brood sorting in ants [25,26] result from the same kind of processes involving local amplification

phenomena (aggregating where we already aggregated, dropping where we already dropped, digging where we already dug) and spatial competition between the resulting structures.

The next step will be to study the structure of the networks. An increasing number of studies suggest that the networks observed at different scales in nature could share common functional properties such as the minimization of distance between two nodes or the robustness to disconnection [27-29]. But networks in nature are not static. The origin of the functional properties of these networks has to be searched for in the processes that govern their growth. Thus a fundamental question remains to be investigated: are there common principles of growth that gives to these various networks structures the same adaptive properties?

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