SHORT COMMUNICATION

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Nest excavation in ants: group size effects on the size and structure of tunneling networks

Abstract Collective digging activity was studied in the ant *Messor sancta* Forel in laboratory conditions and with a two dimensional set-up. We analyzed the digging dynamics and topology of tunneling networks excavated by groups of workers ranging from 50 to 200 individuals over 3 days. In all conditions, the dynamics of excavated sand volume were clearly non-linear. Excavation began with an exponential growth and after 3 days reached a saturation phase in which activity was almost totally stopped. The final volume of sand excavated was positively correlated with the number of workers. At the end of the experiments, the two-dimensional tunneling networks were mapped onto planar graphs where the vertices represent small chambers or intersections between tunnels and the edges represent tunnels. We found that all the networks belonged to a same topological family and exhibited several striking invariants such as the distribution of vertex degree that follows a power law. When increasing the number of ants, some changes occurred in the network structure, mainly an increase in the number of edges and vertices, and the progressive emergence of enlarged and highly connected vertices.

Introduction

Construction behavior in social insects has been the topic of many studies but most of them have focused on epigeous nests built by bees (Darchen 1962; Hepburn 1998),

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wasps (Jeanne 1996; Theraulaz et al. 1998) and termites (Grassé 1959; Bruinsma 1979; Camazine et al. 2001). However, few detailed descriptions of underground tunneling networks exist, though they represent the hypogeous part of the majority of nests built by ants (Tschinkel 1987, 1999a; Cassill et al. 2002; Mikheyev and Tschinkel 2004). A typical underground ant nest is a set of chambers interconnected by a network of tunnels (Délye 1971; Thomé 1972; Brian 1983; Cerdan 1989; Rasse 1999). Nest excavation has a considerable cost for a colony and ants have to coordinate their work in order to build a nest whose size is much larger than that of a single individual. How are these underground structures built and how are they organized, especially when colony size is increasing?

Several field studies have pointed out an important property of the nest structure, namely that, in various species of ants, nest size is adjusted to population (Tschinkel 1987, 1999b; Mikheyev and Tschinkel 2004). This relationship was also found in laboratory conditions, which also makes it possible to investigate the excavation dynamics and thus to provide a better insight on the underlying growth mechanisms (Rasse 1999; Rasse and Deneubourg 2001). As regards the structure, we practically ignore the characteristics of tunneling networks. Thus, a necessary first step is to determine which measures can efficiently describe their main characteristics and secondly to study how they are affected when the population size is changed. One can consider the structure of tunneling networks as a discrete set of interconnected segments of tunnels that can be described by a planar graph. This approach has never been applied to the characterization of tunneling networks built by ants, although it has proved to be a powerful tool to identify invariants in network topology or to categorize different forms of networks (Albert and Barabasi 2002; Solé et al. 2002; Dorogovtsev and Mendes 2003).

In this paper, we analyze the tunneling networks produced over 3 days by groups of 50, 100 and 200 workers of the ant *Messor sancta* Forel in the laboratory. The size of the set-up was the same for the three groups, each group corresponding to a different population density. We

used a horizontal experimental set-up in which excavation took place in two dimensions and in a uniform environment. Tunneling networks were therefore not influenced by the strong heterogeneities found in the natural environment. This set-up enabled us to study: (1) how excavation evolves with time; (2) the relationship between the total volume of sand excavated and the number of ants; (3) the main topological and structural properties of the networks and how these are changed for varying group size.

Materials and methods

We used three colonies composed of workers (population range: 2,000–5,000) and brood collected in southwestern France (Narbonne). The general experimental set-up consisted of a disk of sand 20 cm in diameter and 5 mm in height. We used fine yellow sand, which was poured into a mold and humidified by spraying with water (25 ml). The mold was then removed and the disk of sand covered with 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. Each experiment began with the random dispersal of the ants around the disk. It was then videotaped from above for 3 days in time-lapse mode (2 s every 20 min) with a high-resolution digital camera (Sony DCR-VX1000E). Under these conditions, ants are strongly stimulated to dig. At the end of each experiment, the excavated sand was collected, dried for 1 week at room temperature and subsequently weighed. Three group sizes were tested: 50 ($n=5$), 100 ($n=5$) and 200 ants ($n=10$). Preliminary tests showed that the size of the set-up was large enough to prevent any limitation of the digging activity. To study the dynamics of the excavation, image analysis software developed with Aphelion (http://www.adcis.net/) was used to estimate the volume of excavated sand every 20 min. The software was calibrated by comparing the volume measured by image analysis with the volume of sand collected at the end of the experiment. The topology of the networks was quantified at the end of each experiment using some other software that allowed the identification of the network components. We considered the network as a planar graph $G=(V, E)$ with a set of vertices V characterized by their (x, y) position and diameter, and a set of edges, E, linking pairs of vertices, characterized by their width and length. The edges correspond to the subsections of the tunnels connecting two vertices. Vertices correspond to intersections between the tunnels, to their openings at the periphery of the sand disk (*peripheral vertex*) and to their dead ends inside the sand disk (*front vertex*). Vertex diameter was estimated by fitting a circle to the excavated space on the experimental picture. The vertex degree k_i corresponds to the number of edges connected to the vertex i. When we determined the distribution of degrees for a network, we excluded *peripheral* and *front vertices*. All analyses were conducted with SPSS 11.0 for Windows. Power-law relations were estimated by performing a linear regression on the log–log transformation of the data, and the exponent value of the power law was simply given by the value of the regression coefficient. Note that in the case of a linear relation the exponent value is equal to 1.

Results

Excavation dynamics and regulation of the network volume

In each experiment, the dynamics of excavation was of the logistic type: the excavation rate progressively increased and reached a maximum value after around 15 h; then, after 72 h, the digging rate was negligible, suggesting that the excavated volume should have reached a plateau value (see Fig. 1). This type of kinetics can be described with a double feedback model such as the Verhulst logistic model:

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

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

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

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

Fig. 1 Mean dynamics of excavated volume of sand involving 50, 100 and 200 ants. The *shaded regions* correspond to the SE bars. For each group size an example of tunneling network obtained after 3 days is shown
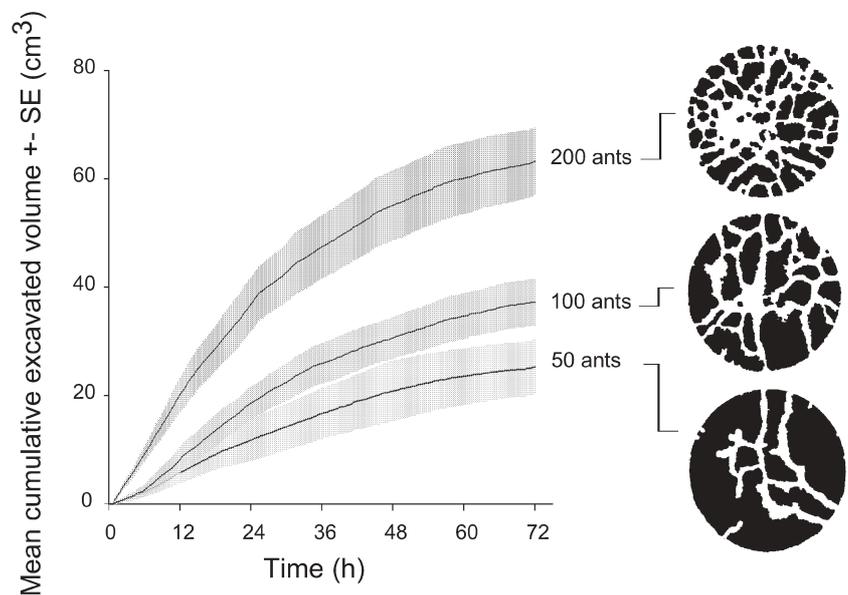
Table 1 Overview of the main characteristics of tunneling networks in terms of volume and topology in the different experimental groups (mean values ± SD, or geometric mean values X/ s*). τ_{max} corresponds to the time at which a maximal excavation rate was reached. $S_{v>2\ cm}/S_v$ represents the ratio between the total surface covered by the vertices with a diameter larger than 2 cm and the total surface covered by all vertices

Network characteristics	50 ants	100 ants	200 ants
	(n=5)	(n=5)	(n=10)
Volume (cm^3)	25.3 ± 11.1	37.6 ± 9.19	68.6 ± 16.5
τ_{max} (h)	15.6 ± 11.7	17.1 ± 5.7	6.2 ± 2.1
Number of vertices (V)	24.2 ± 8.6	35.2 ± 10.1	60.1 ± 20.6
Number of edges (E)	21.0 ± 11.3	37.4 ± 15.4	70.6 ± 31.2
Vertex diameter (cm)	1.04 ^{x}/1.2	1.11 ^{x}/1.3	1.21 ^{x}/1.4
Edge width (cm)	0.69 ^{x}/1.1	0.74 ^{x}/1.1	0.89 ^{x}/1.2
Vertices/Length (cm^{-1})	0.33 ± 0.06	0.30 ± 0.02	0.34 ± 0.04
E/V	0.84 ± 0.10	1.03 ± 0.16	1.13 ± 0.15
$S_{v>2\ cm}/S_v$	0.10 ± 0.22	0.23 ± 0.17	0.47 ± 0.31

$$Ln\left(\frac{(v_s/v_{(t)})-1}{(v_s/v_0)-1}\right) = -\alpha t \qquad (3)$$

Equation (3) was tested by using a linear regression performed on each experiment; the initial volume v_0 was fixed to 1% of the mean final volume v_s measured in the five experiments with 100 ants. This yields a value $v_0=0.375$ cm^3. This logistic model gave a good description of all dynamics ($R^2>0.9$ in all cases). Despite the fact that the mean dynamics erases the logistic shape observed for each experiment, it appears well for 50 and 100 ants (Fig. 1). For 200 ants, the apparent lack of an acceleration phase is due to the high initial excavation rate.

The relation between the number of ants and the total excavated volume after 3 days was best described by a power law with exponent value $\beta=0.752\pm0.11$ SE ($R^2=0.73$; $n=20$; test against slope value $\beta=1$: $t=2.28$; $df=18$; $P=0.035$). This suggests that the total volume of the network is adjusted to the population in an almost linear way, but tends to grow slightly more slowly than the population.

Size and topological properties of the networks

The total numbers of vertices (V) and edges (E) were correlated with group size (Table 1). The relation between the number of vertices and the number of ants (A) was best described by a power law with exponent value $\delta=0.664\pm0.13$ SE ($R^2=0.58$; $n=20$; test against slope value $\delta=1$: $t=-1.9$; $df=18$; $P=0.072$). The distributions of vertex diameter appeared to be log-normal in all experiments (K-S one-sample test, $P>0.05$). The frequency of large vertices ($\emptyset>2$ cm), increased significantly with group size ($\chi^2=8.38$; $df=2$; $P=0.015$; see Table 1). At the same time, the proportion of the total vertex surface covered by these
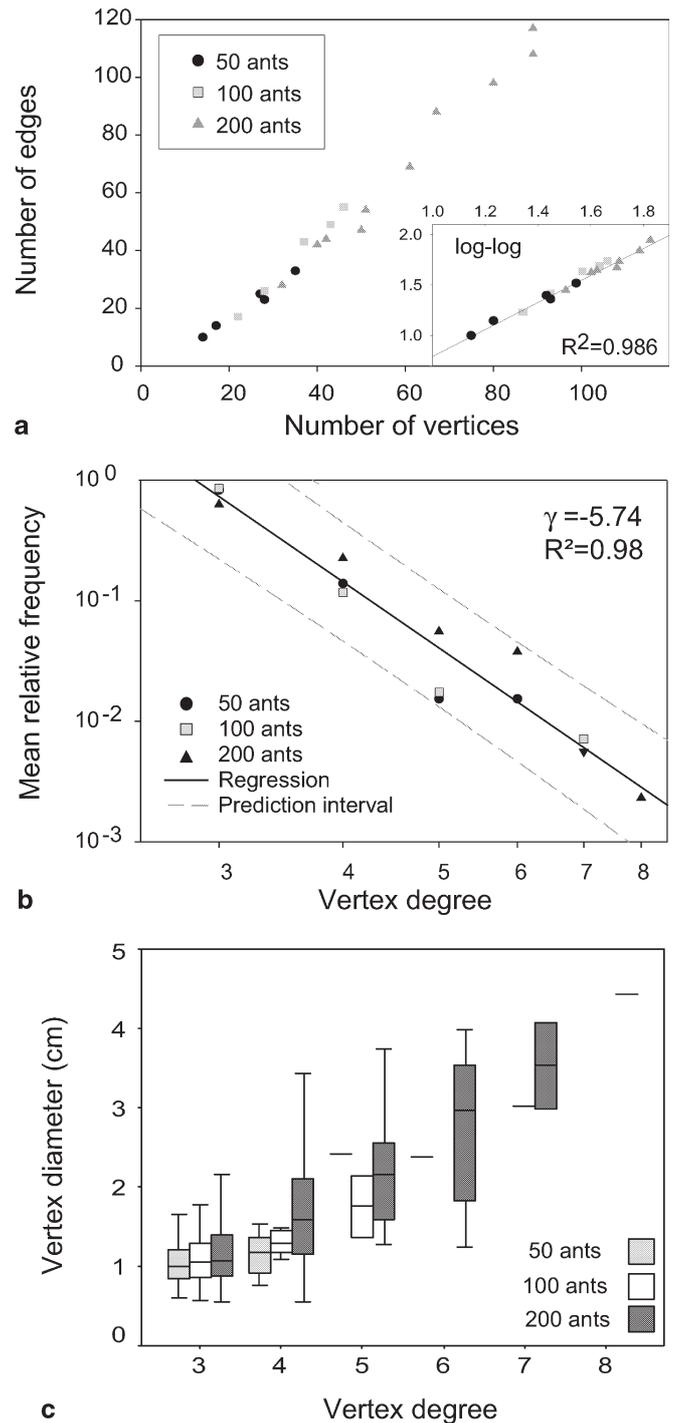
Fig. 2 Topological characteristics of the networks dug by 50, 100 and 200 ants. **a** Relation between the number of edges and the number of vertices. The relation was non-linear and best described by a power law of exponent value $\epsilon=1.31\pm0.036$ SE ($r^2=0.96$; test against slope $\epsilon=1$: $t=8.65$; $df=18$; $P<0.001$). **b** Vertex degree distributions. The *line* corresponds to the linear regression performed on the pooled data transformed in log-log. **c** Relation between the degree and the diameter of the vertices

large vertices was positively correlated with the number of ants (r_s=0.55; n=20; α=0.05; Table 1).

In conjunction with these changes, a number of invariants in the network structure were found. The relation between the number of vertices (V) and the length of the network (L; sum of the lengths of all edges) was linear (power-law exponent: ϕ=1.04±0.07 SE; R^2=0.924; n=20; test against slope ϕ=1: t=0.053; df=18; P=0.96). This indicates that the branching frequency of the tunnels remains constant whatever the ant density (Table 1). When the size of the network increased, the number of edges grew slightly faster than the number of vertices (Fig. 2a). The relation between edges and vertices can be studied more precisely by analyzing the vertex degree distribution, which appeared to be very similar in the three group sizes (Fig. 2b). Indeed, these distributions did not differ significantly (analysis of contingency table: χ^2=92.6; df=95; P=0.55). The vertex degree distribution was a clear invariant of the network structure and was best described by a power law with a negative exponent value γ=−5.74 (R^2=0.98; Fig. 2b).

Moreover, there was a significant correlation between a vertex diameter and its degree in groups of 100 (r_s=0.34; n=89; P=0.001) and 200 ants (r_s=0.49; n=312; P<0.001). The relation was not tested in the group of 50 ants because the sample size was too small. The tendency was similar in all groups (Fig. 2c). The difference between groups was due to the fact that the more ants that were involved, the more often vertices with both greater diameter and greater degree were observed.

Discussion

In this study, we showed the existence of several regularities in the tunneling networks built in a standardized set-up by groups of workers of the ant *Messor sancta*. The dynamics of excavation were logistic, and excavation activity ended when the total volume of the tunneling network was adjusted to the number of ants. This observation confirms that this property is a common feature among several ant species (Tschinkel 1987, 1999b; Franks and Deneubourg 1997; Rasse and Deneubourg 2001; Mikheyev and Tschinkel 2004). As regards the structure, the increase in the size of the network not only leads to an increase in the number of its components, i.e., vertices and edges, but also to an increase in the size and the degree of connectivity of a small fraction of vertices. Though their frequency was low, these vertices contributed to nearly 50% of the total surface covered by the vertices in large group size (200 ants). A similar effect has been observed in field studies with the ant *Prenolepis imparis* (Tschinkel 1987) and with *Formica pallidefulva* (Mikheyev and Tschinkel 2004). However, in our experiments, performed with a finite sand area, this effect did not translate into deep changes in the network topology. Several characteristics of the connection pattern, such as the spatial frequency of vertices, the vertex degree distributions, or the relationship between vertex degree and diameter followed invariant laws. It is interesting to speculate whether such invariants would also be found in large-scale networks.

The regularities of these tunneling networks are the result of growth processes. To understand the emergence of these structures, the mechanisms underlying their construction remain to be studied. As regards the mechanisms underlying volume regulation, the positive feedback observed in the growth dynamics could result from a recruitment process. The tendency for an individual to dig where other individuals have previously dug has been shown in several ant species (Hangartner 1969; Imamura 1982; Rasse 1999). It could be based on chemical communication involving alarm pheromones (Wilson 1958; Imamura 1982; Blum 1996) or CO_2 (Hangartner 1969; Rasse 1999). As regards the progressive decrease in activity at the end of the excavation dynamics, two types of mechanisms could be involved: the first corresponds to a direct triggering of the termination of digging activity through the perception of specific signals by individuals, such as the CO_2 concentration (Deneubourg and Franks 1995; Cox and Blanchard 2000) or the encounter rate between ants (Gordon et al. 1993; see also Nicolis et al. 2004). The second relies on the propagation properties of the recruitment process that would lead the activity to stop at a particular density of ants (Deneubourg and Franks 1995). A recent study in *Lasius niger* (Rasse 1999; Rasse and Deneubourg 2001) suggests that this second mechanism could be involved. However, no studies and, in particular, no models have tested whether the recruitment process alone can actually lead to a linear adjustment of the excavated volume to the number of ants. Special attention should be given to testing these hypotheses. Many questions remain open concerning the emergence of the regularities observed in the structure of tunneling networks. Although several detailed studies have described the behavior and digging patterns of isolated workers (Sudd 1969, 1970a, 1970b), several structures, such as bifurcations and chambers, are never observed when only one or a few individuals are involved. Therefore, it is important to study how the interactions among individuals give rise to a particular tunneling network pattern.

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