

Dynamics of Nest Excavation and Nest Size Regulation of *Lasius niger* (Hymenoptera: Formicidae)

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Accepted April 28, 2000; revised February 12, 2001

*The adaptation of nest size to its population is one of the most common processes, but little is known about the dynamics nest-building and -enlarging in social context. Furthermore, the mechanisms involved remain totally ignored. We present here the first results of such dynamics in the context of *Lasius niger*'s nest excavation. We find, with an artificial but standardized method, a strong positive correlation between the number of ants and the final nest volume as well as the digging rate. Both grow almost proportionally to population. When the number of individuals is artificially increased (even slightly) in a nest, its dimension is systematically adjusted in the same way as initial excavation. In this process, digging acts as a negative feedback that controls nest enlargement. Experiments revealed that this negative control is due directly to the volume of the nest as well as the physiological or behavioral modification of ants after digging. Finally, amplification of activity was observed during the enlargement phase, suggesting the possible implication of self-organized processes in the volume control mechanism.*

KEY WORDS: ants; *Lasius niger*; nest; digging; size regulation; dynamics.

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INTRODUCTION

Among ants, nests are produced by the majority of species and are highly variable in form and size (Brian, 1983; Hansell, 1984). Nonetheless, within a particular species and context (soil conditions, for example), the relation between nest size and population is relatively constant. This has been verified in epigeous ant nests (Tschinkel, 1993, 1999; Franks *et al.*, 1992) as well as in other groups of social insects such as termites (Lepage, 1974; Collins, 1981) and bees (Darchen, 1959). Very little is known about the regulation of nest size except for simplified situations (Bruinsma, 1979; Franks and Deneubourg, 1997). Even less is known about subterranean nest structures. Nevertheless, the study of digging presents the advantage that the volume excavated can be estimated at any time by weighing soil deposited at the surface.

In this context, our objectives are to characterize the dynamics of nest excavation as well as the adjustment of volume dug as the function of number workers. To achieve this, *Lasius niger* is a convenient insect to use because this ant builds mainly subterranean nests, much is known about its biology (Lenoir, 1979; Hölldobler and Wilson, 1990), and it can be easily collected and maintained in the laboratory.

We have developed standardised procedures for systematically examining the regulation of nest excavation.

MATERIALS AND METHODS

Ants were collected in April (one colony) and October (one colony) 1995, and controls in April 1996 (two colonies). Due to possible differences between these groups, experiments (begun in May and December 1995 for the first set) were systematically separated. The colonies (without queens and brood) were installed in boxes with tubes, within which the ants could live. The photoperiod in the laboratory was about 12 h, with lights-on at 0800. Food consisted of pieces of a solid preparation (Bathkar and Withcomb, 1970). Group activity was followed during several weeks. In these experiments, the ant groups were initially placed in a petri dish ($\phi = 15$ cm) and had access to a sand bucket through a single hole in the center of the dish ($\phi = 0.5$ cm). In this humid Brusselean sand (tertiary deposit, 5 kg, humidified at 15% in mass), a group of workers could establish their nest. In each experiment, we measured the daily weight of excavated sand brought to the surface by the ants and deposited in the petri dish [1 g of dried sand = 0.67 ± 0.0001 cm³ (SD)].

Experimental Procedures

Dynamics of Digging by Groups of Different Sizes

As our reference group, we first studied the digging activity of 50 workers [$n = 11$ (5 experiments in May + 6 in December 1995)]. Then we studied the excavation of groups composed of 25 [$n = 11$; 7 (May 1995) + 4 (December 1995)] 100 [$n = 6$; 4 (May 1995) + 2 (December 1995)] and 150 ants [$n = 1$ (May 1995)].

Effect of Population Increases on Nest Volume

After several weeks, the nest volume stabilized. We then artificially increased the population and followed the resulting volume of material excavated. We added groups of different numbers of ants (25, 50, 100, and 150 ants of the same colony) to the initial groups (25, 50, 100, and 150 ants). To get a global view of the phenomenon, we favored using a diversity of combinations rather than repeating a few (Table I).

Moreover, after the addition of ants to the initial groups, we followed the activity of both groups: the initial one (experiments with 50 workers, not marked) and the added individuals (marked). The combinations studied were 50 ants + 10, 25, 50, 100, and 150 ants. Among these, two were repeated twice (50+50 and 50+150). We marked ants the day before their introduction in the nest, with scale model paint (Humbrol-Enamel) applied on their abdomen. Measurements were taken from a video recorder that regularly filmed the nest entrance before and after the ants were introduced, the recordings lasting 10 min. To focus on the digging activation, the intervals were of 1 h during the first 8 h. Afterward, the intervals were of 3 h during 10 days.

Table I. The Different Combinations of Initial and Added Populations in the Nest; The Number of Repetitions Is Indicated for Each Experiment

Added population	Initial population			
	25 ants	50 ants	100 ants	150 ants
10 ants	— (2) ^a	— (1)	— (1)	—
25 ants	1 (2)	1 (1)	1 (1)	—
50 ants	1 (—)	2 (2)	1 (—)	—
100 ants	1 (—)	1 (1)	1 (—)	—
150 ants	2 (—)	1 (1)	1 (—)	1
Repetitions	5 (4)	5 (6)	4 (2)	1

^aValues for December 1995 in parentheses.

To check if these measurements were compatible with the quantities of sand weighed daily (corresponding to the effective activity), we estimated from the video recording the volume dug in 10 days. To do this, we extrapolated the excavated mass during one transport [$3.13 \cdot 10^{-4}$ g (2336 grains excavated weigh 0.73 g)] to the 10 days of the experiment. This was accomplished by averaging day by day the number of transports during the 10 min of recording every 3 h. In the seven experiments the ratio between weighed sand to the calculated quantity excavated was close to 1 [0.89 ± 0.32 (SD)], validating the method.

Examination of Factors Responsible for the Digging Dynamics

Three series of experiments allowed us to evaluate the effects of previous experience and to assess the influence of a previously dug nest on naïve ants. The experimental setup was similar to the previous one except for the number of workers (10), the petri dish diameter ($\phi = 8.5$ cm), and the sand bucket, which contained only 250 g of moist sand.

Series 1 consisted of experiments after which ants were removed from the dug nest and replaced in the initial condition (in the petri dish of a new setup) [$n = 8$ (July 1996)].

Series 2 consisted of naïve ants placed in a container in which a nest had been dug previously by another group, which was removed before [$n = 8$ (July 1996)].

Series 3 consisted of experiments after which ants were also extracted from their nest but either replaced in another dug nest [$n = 8$ (August 1996)] or replaced in their own nest ($n = 4$).

RESULTS

Dynamics of Digging

For the reference group of 50 ants, the nest volume grows monotonically, reaching a plateau value after a few dozen days (volume V_S), while the digging rate reaches its maximum on the first day and decreases as the volume V approaches the plateau value (Fig. 1A). With other group sizes, the dynamics are similar to that seen with 50 individuals (Fig. 1A), while quantitatively the maximal rate (α) and the plateau volume (V_S) grow with the population.

Such dynamics suggests that the digging rate (dV/dt) decreases as the volume V approaches V_S . The excavated volume acts as a negative feedback on the dynamics and the dynamics suggests that the relationship between the

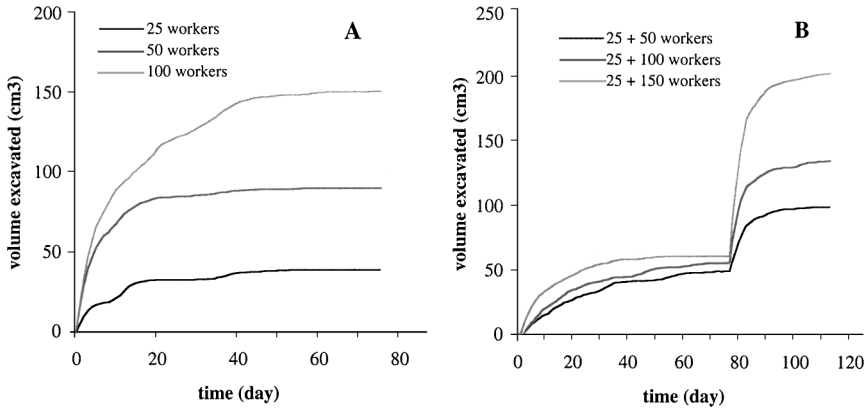


Fig. 1. (A) Time evolution of the accumulated mass excavated by three groups of different sizes: 25, 50, and 100 workers: May 1995. (B) Dynamics resulting from nest enlargement after population increases: 25 + 25, 25 + 50, and 25 + 100 workers.

digging rate and the excavated volume is

$$\frac{dV}{dt} = \alpha \left(1 - \frac{V}{V_S} \right) \tag{1}$$

which, when solved, gives

$$V = V_S(1 - e^{-(\alpha t/V_S)}) \tag{2}$$

The fitting reveals the high values of the regression coefficient (see Table II), which validate the model. Afterward, to characterize quantitatively the relationship between the group size (N) and the volume (V_S), and

Table II. For Each Population, the Number of Experimental Repetitions (n), the Mean Final Volume Excavated ($V_S \pm$ SD), the Maximal Rate (α), and Its Minimal r^2

Date	Population (No. of ants)	n	Final volume, V_S (cm ³)	Maximal rate, α (cm ³ day ⁻¹)	r^2_{\min}
May 1995	25	7	51.7 ± 7.8	4.2 ± 1.3	0.91
	50	5	96.6 ± 12.1	7.9 ± 1.3	0.86
	100	4	147.1 ± 20.5	11.4 ± 2.9	0.85
	150	1	196.7	15.7	0.88
December 1995	25	4	10.1 ± 3.8	0.8 ± 0.7	0.88
	50	6	26.5 ± 4.4	1.7 ± 0.9	0.83
	100	5	33.4 ± 10.5	2.6 ± 1.0	0.94

the maximal rate (α), we first fit with the following equation:

$$V_S = \gamma N^\beta \tag{3}$$

where γ is the volume dug per individual and β characterizes the relation between group size (N) and V_S (proportional relationship if $\beta = 1$). One obtains a β close to (statistically not different from) 1 while smaller than 1 (0.77) (Fig. 2A, Table III).

As far as the volume and its relation to the population are concerned, we can deal similarly with the maximal digging rate, using the same kind of equation:

$$\alpha = \delta N^\varepsilon \tag{4}$$

It appears that α is also almost proportional to the group size, although it increases at a lower rate than the number of ants ($\varepsilon = 0.73$). Nevertheless, ε cannot be considered to be statistically different from 1 (Fig. 2C, Table III).

Seasonal or Colonial Effects

Experiments in May and December 1995, realized with two colonies, present significant differences (Figs. 2A and C). The maximal digging rate and the plateau volume are higher in May. One can also notice that if the season or the colony does not affect β and ε , it does affect the individual volume γ (which is four times smaller in December) and the individual rate δ (which is eight times smaller in December) (Figs. 2A and C, Table III).

Therefore these experiments indicate that (1) the volume excavated exerts a negative feedback on the activity, and (2) the final equation volume

Table III. Values of the Parameters Characterizing the Final Volume (V_S) and the Maximal Rate (α) as a Function of the Population Size^a

V_S	Phase	n	β	γ (cm ³ ant ⁻¹)	r^2	P
May 1995	Initial digging	17	0.77	4.4	0.93	<0.001
	Adjustment	15	0.77	3.5	0.87	<0.001
December 1995	Initial digging	15	0.75	1.1	0.55	<0.001
	Adjustment	12	0.84	0.9	0.79	<0.001
α	Phase	n	ε	δ (cm ³ ant ⁻¹ day ⁻¹)	r^2	P
May 1995	Initial digging	17	0.73	0.46	0.79	<0.001
	Adjustment	14	0.56	1.61	0.48	<0.01
December 1995	Initial digging	15	0.86	0.07	0.44	<0.01
	Adjustment	12	1.22	0.01	0.48	<0.01

^aThe parameters were Obtained by fitting $\ln V_S$ and $\ln \alpha$ as a function of $\ln(\text{population})$.

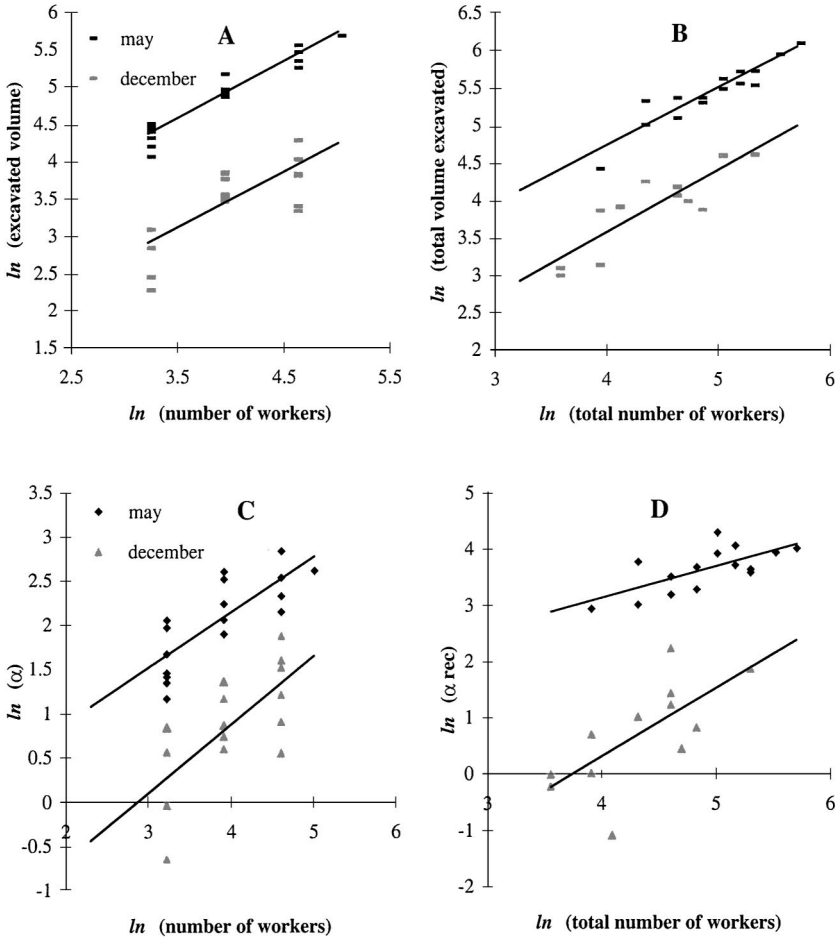


Fig. 2. (A) A log–log representation of nest size (V_S) as a function of population size (N), for May ($y = 0.77x + 1.88; r^2 = 0.93$) and December ($y = 0.75x + 0.51; r^2 = 0.55$) 1995. (B) A log–log representation of nest size as a function of total population size after population increases, for May ($y = 0.78x + 1.64; r^2 = 0.87$) and December ($y = 0.84x + 0.24; r^2 = 0.79$) 1995. (C) A log–log representation of maximal digging rate (α) as a function of population size (N), for May ($y = 0.73x + 0.52; r^2 = 0.77$) and December ($y = 0.86x - 2.64; r^2 = 0.44$) 1995. (D) A log–log representation of maximal digging rate during the nest adaptation as a function of total population size after population increase, for May ($y = 0.56x + 0.88; r^2 = 0.48$) and December ($y = 1.22x - 4.57; r^2 = 0.48$) 1995.

V_S and the maximal digging rate α are proportional to the group size, although there is a tendency for both to increase more slowly than the number of workers.

Effect of Population Increases on Nest Volume

Experiments in which we increased the number of workers show that (1) the digging is triggered immediately—starting on the first day (Fig. 1B)—even when the added number is low (10%) compared to the initial group size; (2) the dynamics of the nest enlargement is the same as that of the initial excavation, which means that the activity is maximal at the beginning and decreases afterward (Fig. 1B); and (3) both volume and speed grow as a function of the total number of ants (Figs. 2B and D).

In this situation the model [Eq. (1)] is adapted into Eq. (5), taking into account that the initial volume is now equal to V_S , digging leading to a new final volume ($= V_{S_{\text{tot}}}$, corresponding to the new population $N_{\text{tot}} = N + N_{\text{add}}$).

$$\frac{dV_{\text{tot}}}{dt} = \alpha_{\text{rec}} \left(1 - \frac{V_{\text{tot}}}{V_{S_{\text{tot}}}} \right) \quad (5)$$

which gives

$$V_{\text{tot}} = V_{S_{\text{tot}}} - (V_{S_{\text{tot}}} - V_S) e^{-(\alpha_{\text{rec}}/V_{S_{\text{tot}}}) \cdot t} \quad (6)$$

In these equations, time 0 corresponds to the increase in population. We proceed then as we did for the initial phase and fit the dynamics of the experiments to Eq. (6). The different fittings confirm the feedback hypothesis of the model [all $r^2 > 0.80$ (SD = 0.08 for both seasons)]. Once again, the final volume ($V_{S_{\text{tot}}}$) is almost proportional to the total population in the nest (N_{tot}), $\beta = 0.77$ [Figs. 2A and B; Eq. (7a)]. Individual volumes (γ) obtained after enlargements remain constant, confirming the model.

$$V_{S_{\text{tot}}} = \gamma N_{\text{tot}}^\beta \quad (7a)$$

$$\alpha_{\text{rec}} = \delta N_{\text{tot}}^\varepsilon \quad (7b)$$

The estimation of the nonlinearity for the maximal rate α_{rec} , obtained by fittings [Eq. (7b)], shows that the tendency observed during the initial excavation is not so clear anymore, ε being equal to 0.56 ($r^2 = 0.48$).

Seasonal or Colonial Effects

The absence of difference between May and December remains for the exponent β (=0.77 and 0.84), while the difference remains for γ , its value being four times higher in May. For ε , it is equal to 0.56 and 1.22, respectively,

for May and December 1995, but no difference can be considered statistically significant (Fig. 2D). Indeed the maximal digging rate presents an erratic tendency that is even more present when we compare the initial values (α) to those of the population increase (α_{rec}) (Table III).

Thus, these experiments reveal that (1) ants adapt their nest volume to the new population, even when the increase remains weak; (2) as well as for initial digging, the total volume grows proportionally to the population (however, somewhat less); and (3) the maximal rate grows approximately in proportion to the number of ants again, but the volume adjustment V_S is more stable.

When looking at the recorded activities of distinguished groups [initial (unmarked) and added (marked)], the workers' addition reveals immediately that ants in both groups work almost in proportion to their representation in the total population. Nevertheless, the fitting reveals a tendency for initial ants to be less active when the added number increases (Fig. 3).

The initial workers are thus still active, the decrease in their digging rate along time not being caused only by exhaustion. These results are, moreover, compatible with the measurements of mortality, since no more than 10 to 20% of dead ants rejected on the surface were counted. Furthermore, the



Fig. 3. Ratio of sand grains carried by initial group to sand grains carried by added-ants group as a function of the ratio of initial to added workers in the nest population. The number of such transports is an average calculated from 10 min, eight times a day, during 10 days after population increase: $y = 0.40x + 0.33$ ($r^2 = 0.99$).

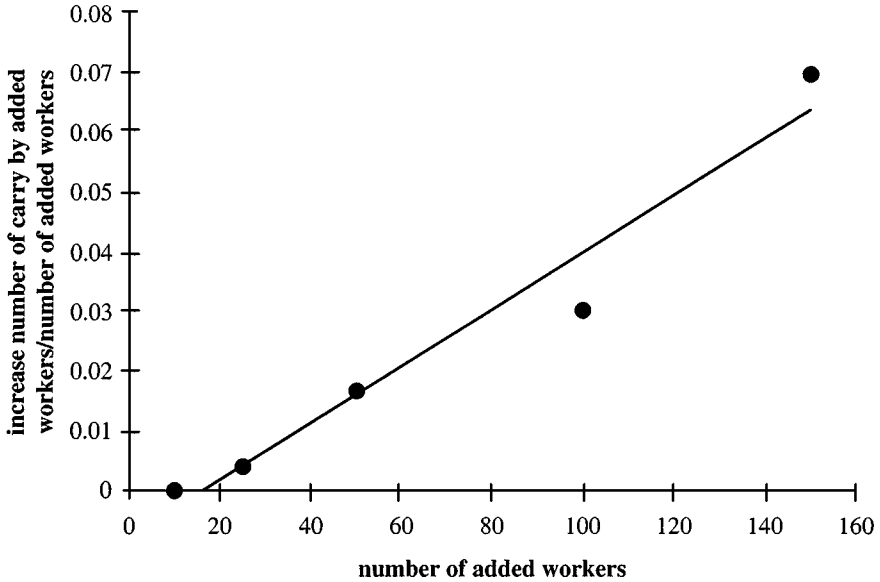


Fig. 4. Linear approximation of transport increase per ants added, as a function of the number of ants added during the first 18 h after population increase. It is realized for the added workers: $y = -5 \cdot 10^{-4}x - 8 \cdot 10^{-4}$ ($r^2 = 0.96$), December 1995.

destruction of the two nests after 120 days showed that both initial populations (50) were slightly affected (42 and 48 ants alive).

If we focus on the first hours (20 h) after the addition, we observe that added ants accelerate their activity more when they are more numerous (Fig. 4). Nevertheless, this acceleration, defined as the increase in transport per ant per minute, is not observed in the initial group. We suppose that the aggregation of initial ants in the nest and their spatial distribution, which contrast with the mobility and the spreading of added ants, are responsible for this erratic activation.

In conclusion, we can say that there is an adjustment of the nest size to the population, corresponding to a new steady volume ($V_{S_{tot}}$). We now shed some light on the mechanisms of this activity decrease.

Factors Responsible for the Digging Dynamics

First, the initial excavations of groups of 10 ants in smaller sand buckets remains similar (Figs. 5A, a, and B, a), the nest volume reaching a plateau after about 20 days for both series. The use of the model [Eq. (1)] gives us

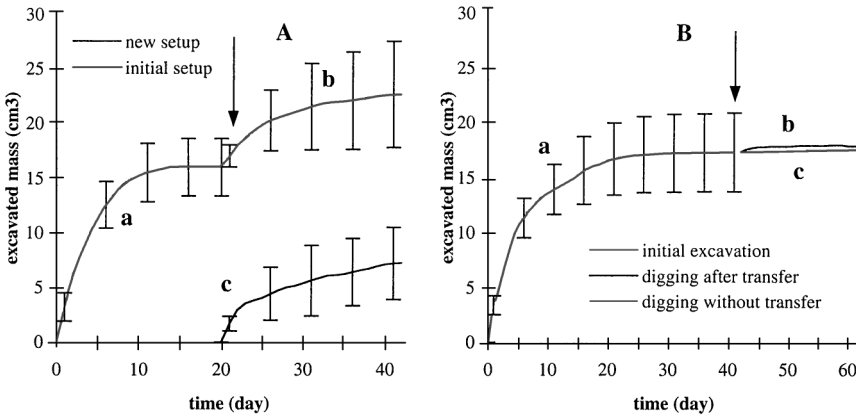


Fig. 5. (A) Mean dynamics ($n = 8$ experiments) of initial excavation by 10 ants (a) and of when they are put back in initial conditions (new setup) (c). We also measured this evolution when naïve workers are introduced into an already dug nest (b). (B) Mean dynamics ($n = 12$) of initial excavation by 10 ants (a) and when they are extracted and reintroduced into their own nest (b) or into an other nest (c).

the final volume V_S and the maximal rate α (Table IV). Compared to the values obtained in May 1995, the volumes V_S per individual appear to be comparable (from Tables II and IV).

In Series 1, the volume excavated by ants after having already dug is about 48% lower than that the first time (taking the mortality into account) (Fig. 5A, c). The maximal rate (α) is also lower, reduced by 82% on average (Table IV). This shows that ants are affected directly by digging (physiological or behavioral change).

In Series 2, when 10 naïve workers are introduced into an empty nest, they dig less than during the initial nest excavation (Fig. 5A, b), and there are also decreases in the V_S (54% less) and α (75% less) (Table IV). This reveals that the volume already excavated is an inhibitor. Nevertheless, the inhibition is not absolute since the naïves still excavate.

In Series 3, when ants are extracted from their initial nest and introduced into another nest (emptied), they dig very weakly (95% weaker) (Fig. 5B, b). We obtain a similar result in Series 4, when, as a control, ants are placed back in their original nest (99% weaker) (Fig. 5B, c). In this case, the absence of activity results from the combination of both effects (previous experience and volume).

In addition, no correlation between the masses initially excavated and either that dug in the new setup ($r^2 = 0.11$) or the mortality is found. This means that if the digging affects ants, it can also depend heavily on the general experimental conditions.

Table IV. Parameters Estimated from the Initial Digging by 10 Workers in Small Sand Buckets (\pm SD)^a

Date	Phase	Population (No. of ants)	Final volume, V_S (cm ³)	Final volume, ant (cm ³ ant ⁻¹)	Max. rate, α (cm ³ day ⁻¹)	Max. rate, α /ant (cm ³ ant ⁻¹ day ⁻¹)
July 1996	Initial ($n = 8$)	10	16.8 \pm 2.9	1.68 \pm 0.30	4.74 \pm 1.97	0.47 \pm 0.20
	Series 1 ($n = 8$)	7.4 \pm 1.1	6.5 \pm 2.7	0.88 \pm 0.20	0.84 \pm 0.48	0.08 \pm 0.05
August 1996	Series 2 ($n = 8$)	10	6.2 \pm 4.6	0.60 \pm 0.46	1.17 \pm 0.87	0.12 \pm 0.09
	Initial ($n = 12$)	10	17.4 \pm 3.6	1.74 \pm 0.36	3.27 \pm 0.98	0.32 \pm 0.01
	Series 3 ($n = 8$)	7.0 \pm 1.4	0.6 \pm 0.5	0.09 \pm 0.07	—	—
	Series 4 ($n = 4$)	7.1 \pm 2.1	0.2 \pm 0.3	0.03 \pm 0.04	—	—

^aAlso presented are those estimated from excavation after dropping old ants into new setups (Series 1) and naive ants into already dug setups (Series 2). In parallel we present the results of ants having dug once and then been introduced into other dug nests (Series 3) or reintroduced into their own (Series 4).

In conclusion, this part of our work reveals that the decrease in activity in the digging dynamics is generated mostly by the combination of two effects: modification of the workers' state and inhibition by the volume. The latter is, nevertheless, not absolute since we detect a tendency for naïve workers to dig even though the nest has reached the proper size.

DISCUSSION

This study of nest-digging regulation has highlighted the following. (1) Digging activity always decreases with time, the nest reaching a plateau volume. The rate of digging is initially high and then decreases after a few days, becoming negligible. (2) Both this plateau (V_S) and the maximal digging rate (α) are closely proportional to the group size. (3) Nests are systematically enlarged when the ant population is increased. This enlarged nest volume is adapted to the new group size, while the dynamics of excavation remains similar to the initial one.

The quantitative variation between different groups of experiments may be due to colonial differences, but our results suggest a dominance of seasonal effect: the final volume per ant is systematically higher for experiments with ants collected in spring (1995 and 1996; experiments in spring and summer) than in autumn (1995; experiments in winter). Such an effect is in agreement with enlargement and repair of the nest under natural conditions occurring in spring and summer. This could be due either to weather conditions, which in this period could stimulate the activity level of individuals, or to the physiological state of the ants, those collected in autumn being less active before their hibernation.

During the enlargement, ants of the initial population and added ants were observed to dig at the same maximal rate. This means that the initial ants can still excavate, but as we have also shown, digging activity is reduced after a previous experience, pointing to the possibility of physiological (Fewell and Page, 1999) or behavioral changes. This contribution is not exclusive since we have revealed that volume inhibits digging. Experimental and theoretical results suggest that the digging rate decreases proportionally when the volume approaches the plateau (V_S).

If we now look at the final volume (V_S) that must be considered, for each set of experiments, as statistically proportional to the population (December–May; initial digging–enlargement), we observe that all the fittings present the same tendency, which suggests that the final volume increases more slowly than the number of workers (population^{0.75}).

The relation between the maximal digging rate and the population size is also nearly linear but presents a higher variability (particularly for the nest

enlargements) than that linking the excavated volume and the group size. This may be due to the fact that rate is a daily value, while volume is a sum of all these daily activities. Thus, the rate (and its calculation) is more sensitive to perturbation from outside or inside the nest. When new ants are added, the spatial distribution of workers within the nest can thus be the origin of the variability observed during the enlargement. Such an effect would be present, in particular, if a digging recruitment is involved. These results lead us to the mechanisms of this regulation and the information processed by ants. Two types of mechanisms can be hypothesized.

In the first hypothesis the individual volume directly triggers the digging activity. This could occur if the ants perceive a particular cue that varies in proportion to the density of workers within the nest. The workers modulate their building activities—always with respect to a given individual volume—as a function of the number of ants and the volume available (Deneubourg and Franks, 1995). After the enlargement, the population density decrease will be detected and excavation will be stopped. The regulation of the *Leptothorax* nest and the size regulation of the royal cell in termites, *Macrotermes* (Bruinsma, 1979; Franks *et al.*, 1992; Deneubourg and Franks, 1995; Bonabeau *et al.*, 1998; Camazine *et al.*, 2001), are examples of such a process.

One possibility for such a cue is a chemical signal whose concentration increases with the group size and decreases with the nest enlargement. The higher the chemical concentration, the more individuals would be stimulated to dig. As a consequence of the digging activity, the concentration and then the stimulation would decrease when the nest reaches a particular volume. Possible chemical cues are a pheromone or a metabolic by-product of the ants' activity, such as carbon dioxide. CO₂ would then be a global state indicator for the worker activity, physiological state, and population size. In particular, its production depends on the physiological state of workers and colonial and seasonal conditions (Hantgardner, 1969; Kleindeidam and Tautz, 1996; Burkhardt, 1998; Lechner, 1995; Burkhardt, 1991, cited by Burkhardt, 1998). With regard to data on this hypothesis, Gallé (1978) has shown that oxygen consumption in a group increases as the volume does, proportionally to group size^{0.75}. It is then reasonable to suppose that if the consumption decreases, the metabolism and its by-products are affected too. Nevertheless, the same nonlinear tendency suggested by our measures must be highlighted, as well as the influence of CO₂ on *Lasius niger*. Other signals could also be involved in this volume regulation, such as the frequency of contacts (Gordon *et al.*, 1993).

In the second hypothesis, the population density does not directly affect the digging behavior of ants. Due to the presence of digging amplification processes such as recruitment for excavation activity, the propagation

of excavation itself (i.e., collective enlargement) depends on the population density. Our results strongly suggest the presence of such a recruitment. Indeed, the measurements during population increase show an acceleration of the activity with the number of ants added. Besides, the exponential dynamics of excavation during the first hours (initial phase) constitutes the typical signature of such positive feedback (Rasse and Deneubourg, 2001). Moreover, in experiments in which ants are given the opportunity to dig at two sites (Rasse and Deneubourg, 2001), groups focused their activity systematically on one of them, which can be interpreted only in terms of amplification processes (Deneubourg and Goss, 1989; Bonabeau *et al.*, 1996; Camazine *et al.*, 2001). Finally, these recruitments are well known in building activities of many social species (e.g., Grassé, 1959; Deneubourg, 1977; Bruinsma, 1979; Skerka *et al.*, 1990; Bonabeau *et al.*, 1997; Camazine *et al.*, 2001) and occurs in *Lasius niger*. In the nest regulation, a global nest enlargement will result from the propagation at the collective level of digging activity, favored by a high worker density. The population density decrease resulting from this excavation will affect this recruitment, until the activity stops. Thus, in this regulation model, such spatial amplification mechanisms could play an essential role in the activation and coordination of digging activity of workers.

These results suppose that regulation, or a part of it, would be based on an indirect inhibition of the positive feedback without involving explicit coding of nest size as in the previous scenario (Deneubourg and Franks, 1995). Population density would not be measured but would be a condition for the initiation, propagation, and collective nest enlargement. The nest size would then be implicitly coded within the dynamics of the propagation itself and these mechanisms would contain their own inhibition.

With regard to our results, the first hypothesis is not verified, while the second would be plausible only when considering the two opposite feedbacks. The first is the amplification for digging, which acts as a short-term positive feedback. It would be inhibited afterward by the volume effect. This long-term inhibiting effect could hide another positive feedback, antagonistic to the recruitment: self-aggregation. The tendency of individuals to self-aggregate is an example of such an inhibitor that would be favored by the nest enlargement. From this point of view, the quantitative description of the long-term activation by our theoretical model and its inability to describe short-term activation confirm these two scales of actions.

ACKNOWLEDGMENTS

This research was generously supported by the Institut pour la Recherche Scientifique dans l'Industrie et l'Agronomie, the Fonds pour la

formation à la Recherche dans l'Industrie et dans l'Agriculture, the Future & Emerging Technologies Program of the European Commission, and the Fondation David et Alice van Buuren. We also thank the referees and, especially, Scott Camazine for his suggestions and the time he spent editing the paper.

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