

Research article

Nest architecture of the ant *Formica pallidefulva*: structure, costs and rules of excavation

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Summary. The architecture of underground ant nests was studied in the ant *Formica pallidefulva*. These ants build shallow (30–45 cm deep) nests, which consist of more or less vertical shafts that bear chambers. Shafts are modular units of nest growth; nests are enlarged by adding more shafts or extending previously existing ones. The nests are top-heavy, their volume declining exponentially with depth. The total volume of the nest is strongly correlated with the number of worker occupying the nest ($R^2 = 0.87$). Some of the rules and templates used by workers for nest construction were determined: (a) chambers are formed in the direction of the tunnels leading up to them, (b) the amount of soil excavated per unit time increases with soil temperature and moisture content. The amount of time and energy required to construct a typical nest were approximated using digging ability parameters determined in the lab. We estimate that if a colony was to move twice a year, it would expend around 20% of its energy intake and at least 6% of its worker time on nest excavation.

Key words: Chambers, tunnels, orientation, Polyergus.

Introduction

Much of an ant's life passes inside the nest, whose relative security conceals the queen, piles of brood and, seasonally, the reproductives. The location of the nest influences many aspects of the ants' ecology and behavior. For example, weaver ants make their homes out of living leaves and never leave the forest canopy (Hölldobler and Wilson, 1983). Tramp species such as the pharaoh's ant can do with almost any crevice and became pandemic after centuries of traveling with human cargo (Vail and Williams, 1994). However, most ants live in the soil, shaping their underground nests by excavation (Sudd, 1969). It is evident that these nests

exhibit species-specific patterns, likely of some adaptive value to the ants.

Most studies of social insect nest architecture have focused on nests that are constructed by their inhabitants. Numerous studies describe the structure and construction of paper, mud and wax nests (reviewed by Theraulaz et al., 1998). However, underground excavation has received much less attention. Although the number of accounts mentioning ant nest architecture is considerable, most of them have been qualitative descriptions, at best accompanied by sketches (Talbot and Kennedy, 1940; Autuori, 1942; Talbot, 1948; Scherba, 1961; Ettershank, 1968; Kondoh, 1968; Lavigne, 1969; Wheeler and Rissing, 1975; Dlusskii, 1981; MacKay, 1981; Kugler and Hincapie, 1983; Tschinkel, 1987; Bristow et al., 1992; Crosland, 1995). Any sort of quantitative data on ant nests have been scarce (however, see Tschinkel (1987, 1999); Cassill et al. (2002)).

All of the described underground nests have the same basic ground plan, consisting of chambers, which typically contain brood and workers, and tunnels, which provide connections between them. Except for fungus gardening ants, which have roughly spherical chambers (Wheeler, 1907), the chambers of most ants are vertically flattened. Usually, chambers are vertically stratified, offering different temperature and humidity regimes. The depths of nests vary considerably from a few centimeters in tropical or temperate zone ants (e.g., Williams and Logfren, 1988) to several meters (Kondoh, 1968; Tschinkel, 1987). The deepest nests, over four meters, have been found in desert-dwelling ants, which need to access the water bearing layers of the soil (Dlusskii, 1981).

Describing the architecture of termite mounds, Emerson (1938) pointed out that social insect nests are morphological expressions of behavioral patterns on the scale of the entire colony. In large societies, where hundreds or thousands of workers collaborate on the construction of a nest, individual variation is almost completely cancelled out (Emerson, 1938). Thus, the ants' underground structures are the culmi-

nation of effort put into excavation by numerous workers, governed not by a blueprint but by rules innate to every individual. Yet, few studies have focused on the rules that govern the excavation of ant nests. Although the behavioral sequences by which ants carve, pack and remove soil from the nest have been well characterized (Sudd, 1969; Dlusskii, 1981), little is known about how these simple behavioral patterns are integrated, giving rise to the entire nest structure. Sudd (1969, 1975) reconstructed species-specific tunnel shapes based on solitary workers digging. Although these trials to some extent succeeded in reproducing species-specific tunnel patterns, no chambers were ever formed. Furthermore, the results of single worker experiments did not readily scale to larger group sizes, due to increased social complexity caused by the introduction of even one more worker (Sudd, 1972).

Unlike the usual case in organization of human societies, there exists no centralized controller governing of the excavation of ant nests. By necessity workers need to respond to local environmental cues in order to guide their activity. Possible environmental templates that may direct ants in patterning their nests include temperature, moisture and carbon dioxide concentration gradients in the soil. Indeed, *Myrmica rubra*, *Formica polyctena* (Ceusters, 1986) and *Solenopsis invicta* (Porter, 1993) workers position themselves within a nest in response to temperature gradients, while workers of the desert ant *Messor eburnius* dig towards increased water concentrations (Thomé, 1972) and carbon dioxide was found to release digging behavior in the fire ant *Solenopsis geminata* (Hangartner, 1969).

Given the size and complexity of many ant nests, the ants no doubt expend considerable effort and energy in excavating them. Yet, estimates of the cost of nest excavation have been severely limited by the lack of quantitative data on ant nests, especially in conjunction with estimates of behavioral parameters such as load sizes and the digging speeds (however, see Sudd and Franks (1987) for an attempt at estimating the energetic cost of excavation).

In the present study we set out to investigate prominent features of the nest architecture of one ant species. Then, we looked at some of the rules ants may use to create such a nest, and the environmental factors that may act as templates that guide construction. Finally, we estimated the costs of *de novo* nest excavation both in terms of time and energy.

Materials and methods

Our model, *Formica pallidefulva*, is a large reddish-brown ant that is abundant in the southeastern United States (Creighton, 1950). It subsists mostly by scavenging dead insects and other small food items. The nests of two other members belonging to the same species complex were described previously by Talbot (1948).

Nest architecture

The study site was located in the Apalachicola National Forest, approximately fifteen km southwest of Tallahassee, FL. The vegetation consisted of longleaf pine (*Pinus palustris*), as well as a ground cover of

gallberry (*Ilex coriacea* and *Ilex glabra*) and runner oak (*Quercus* sp.). Between 1st and 4th April 2001 twenty-five colonies of *F. pallidefulva* were cast in dental plaster at daybreak, before the onset of foraging. Dental plaster was slurried in lukewarm water and injected under pressure from a squirt bottle into the opening of a nest. These casts were allowed to solidify and were carefully exhumed the following day. The distribution of *F. pallidefulva* is clumped, making it hard to find more than 5–7 colonies in one patch. Thus, it was necessary to cast nests at several nearby (<2 km distance) sites, which were similar in both soil structure and vegetation. Due to the difficulty of making plaster casts in heavily rooted soil, only seventeen casts from five sites were intact enough to be analyzed.

The pieces of each of the nest casts were glued together with epoxy, and the completed cast was measured and photographed. Though missing pieces made it impossible to assemble casts in their entirety, all 'intact' casts were >90% complete by weight.

For descriptive purposes, we use several operational definitions: (a) a chamber was defined as a horizontal feature of the nest, measured on a scale of centimeters, connected to the rest of the nest by no more than one side, (b) any non-horizontal feature of the nest was defined as a tunnel, especially if it connected two chambers, (c) a shaft was defined as a more or less vertical length of tunnel and its associated chambers stretching from the top of the nest all the way to the bottom. The plaster casts were weighed; the number of chambers and shafts were counted. A nest's volume was estimated using two methods. The first method simply used the nests' weight divided by the density of plaster (estimated about 1.3 g/cm³ for the casting conditions employed in this study). Additionally, nests were photographed and cross sectional areas of 5 cm deep intervals were measured. Using the weight data these areas were converted to volumes. The photographic method of estimating volume allowed exploration of volume as a function of depth. Most analyses of the relationship between nest depth and volume were conducted using the convenient but arbitrary scale of 5 cm deep intervals.

The number of root scars and the number of chambers were counted in 5 cm deep intervals from four perpendicular vantage points. The counts were averaged and used as a measure of root density and chamber number per unit depth.

Within each nest, chambers that were not heavily root scarred or that did not merge with other nest structures were selected for detailed study. Variables included aspects of the chamber such as angle (the bisector of the angle that spans a chamber, Fig. 1), as well as depth, maximum height and maximum width. Also, the direction and length of a tunnel leading up to a chamber was measured. Most chambers close to the surface were too diffuse and too heavily root scarred to provide meaningful data in most of the above categories. Exceptionally, heights of the three topmost chambers in every colony were also measured.

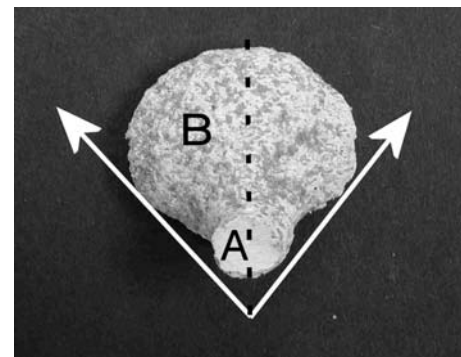


Figure 1. Top view of a nest chamber plaster cast. The angle of the chamber is represented by the dashed line, which bisects the angle between the two arrows going enveloping the chamber. The tunnel leading to the chamber is labeled by A, while the chamber is labeled B

Plaster casts of the nests were then broken down, placed in mesh bags and dissolved in a seawater current over the course of several weeks. The ant heads thus liberated were counted, giving an exact measurement of colony size. Head widths were measured for random samples of 15–20 individuals in each colony.

Excavation

Laboratory experiments were required in order to estimate digging efficiencies of *F. pallidefulva* workers. Colonies of *F. pallidefulva* were kept in plaster nests (plaster dishes covered by glass) under constant light and at 28°C. The ants were provided water, sugar water and mealworm larvae *ad libitum*. Unless specified otherwise, all lab experiments were carried out at 28°C.

Although *F. pallidefulva* workers are monomorphic, they nonetheless exhibit polyethism, with some individuals being fat-laden corpulents, and others fast, lean foragers. In the field, corpulents were never seen digging or foraging. In the nest they were usually found tightly packed in the lower nest chambers, especially in association with brood. Quite likely, the pattern of worker polyethism in *F. pallidefulva* is similar to that of other formicine ants (Kondoh, 1968; Tschinkel, 1987), whose younger corpulent workers stay in the nest, processing food and taking care of the young, while the older workers engage in outside activities.

In practice, except in extreme cases, the distinction between corpulents and foragers is difficult to make. For the analyses below, workers were selected by agitating the colony and collecting workers haphazardly as they scattered from the nest. Though the lean workers were the first to flee, some of the repletes doubtless fled as well. In any case, this procedure produced what appeared to be the colony's most active workers.

'Digging columns' were constructed out of vertical 12.7 cm wide PVC pipes filled with dry sand, which was then moistened to saturation. Mosquito netting on the bottom end of the pipe both held the sand in the pipe and provided adequate drainage for water. Workers were kept in a Petri dish, whose top and bottom were replaced with netting. A conduit of small-bore sand-filled tubing provided access from the meshed enclosure containing the ants to the larger digging tube. A typical trial involved 30 workers chosen from one of the laboratory colonies.

Effects of tunnel orientation on further digging

Workers were induced to dig under two treatments: a vertical $2\sqrt{2}$ cm conduit and a cm long (2 cm high) conduit skewed at a 45° angle to the horizontal (Fig. 2). A nail was pushed 3 cm into the conduit to encourage digging. In other words, while the direction of motion was provided by the conduit, the actual direction of excavation was not constrained. After six h of digging the nest was exhumed and the depth and direction of the chamber were recorded.

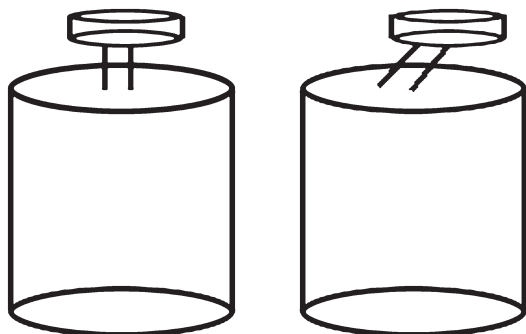


Figure 2. Experimental setup for the digging experiments. Ants were loaded into the upper cylinder (lined with insect netting). Conduits connected the meshed arena with the lower cylinder filled with sand. The conduit could be either vertical (left) or skewed at (right)

Load size estimation

Workers were filmed for one hour while digging. Afterwards, the excavated sand lying below the meshed enclosure was collected and weighed. The number of loads brought out by the workers was estimated from video playback and used to determine the average load size. For the sake of comparison, the average weight of a *F. pallidefulva* worker was estimated by weighing 20 cold-anaesthetized individuals.

Digging time

The conduit connecting the meshed Petri dish and the sand-filled PVC pipe was made of 1.5 cm diameter transparent tubing, which was lined with mosquito netting to facilitate ant movement. The tubing was covered in pink shrink-wrap to minimize disturbance from light. A worker's journey could be seen from the surface all the way to the site of digging at the bottom of the conduit. The round trip time (total time digging and traveling through the conduit) was measured for depths of five and fifteen cm. If self-grooming or interactions with other workers interrupted the focal digger's movement, the trip was not included in the analysis. Ten workers, haphazardly selected from a colony, were placed into the digging arena at a time. Ants were aspirated after completing a round trip and isolated until the end of the experiment while a replacement was introduced to maintain a constant number of workers.

The effect of environmental factors on digging

During the process of excavating a nest, ants are exposed to a variety of gradients present in the soil, such as temperature and carbon dioxide concentration. The effects of temperature, soil moisture and CO₂ on the ants' ability to dig was measured in a CGA/Precision Scientific water jacketed CO₂ incubator. Workers from one large colony were used throughout the CO₂ incubator trials. As only one treatment was possible at a time, the colony was kept chilled at approximately 3°C, and the order of the experiments was randomized. Groups of 30 workers were loaded in digging columns. Petri dishes with a 1 cm in diameter holes in the middle were placed directly on the sand. A 1 cm wide 2–3 cm deep tunnel was pushed through the Petri dish openings with a nail in order to entice ants into digging there. After the ants had dug for six h at a set temperature and ambient CO₂ concentration, the sand they excavated was removed and weighed. The difference in wet and dry weight of the sand was used to estimate water content.

Costs of excavating nests

A rough estimate of the gross cost of transporting sand out of the nest (in J km⁻¹) was calculated according to the model developed by Lighton et al. (1987) for trails of foraging ants. While ant mass, load size and running speeds were estimated empirically as described above, oxygen consumption parameters was calculated with the calibration curves provided by Lighton et al. (1987). The distances sand had to be transported were based on the number of loads that needed to be removed from a given depth (previously estimated at 5 cm increments as discussed above). The total energy expenditure included energy spent on all laden and unladen trips.

The running and loading speed of an ant together with data on the number of trips and the depths of excavation were combined to calculate the amount of ant-hours that would be required to excavate a nest of a given depth-volume distribution.

Statistical analysis

Data were analyzed by standard techniques using Minitab (version 12). Whenever appropriate, data were logarithmically transformed to meet statistical assumptions. Spearman's rank correlations were used either for small sample sizes (less than 20) or whenever parametric assumptions could not be met; standard parametric techniques, specified in the text, were used in other cases. Orientations were analyzed with Rayleigh tests of uniformity carried out in Oriana (version 2). The effects of temperature and carbon dioxide were analyzed with an ANCOVA on the weight of sand excavated, with temperature being used as a covariate. All means are given \pm one standard deviation for nor-

mally distributed data. Otherwise, the minimum, maximum and median values are provided.

Results

Nest architecture

As there were no significant differences among the sampling sites with respect to nest volume ($F_{4,16} = 2.2, P > 0.10$) or nest depth ($F_{4,16} = 0.46, p > 0.70$), nest data were pooled among the sites. The distribution of the total number of ants in a nest was significantly non-normal (Kolmogorov-Smirnov, $p < 0.02$) and ranged from 92 to 2,946 ants, median 401. The total number of ants in the nest was positively correlated with the number of shafts ($r = 0.65, p < 0.01$) and the number of chambers ($r = 0.81, p < 0.001$). On the other hand, no strong relationship between nest depth and the number of ants in a colony was detected ($r = 0.45, p = 0.066$).

The volume of a nest was closely related to colony size ($R^2 = 0.87$), as can be seen in Figure 3. The slope of the regression of nest volume on worker number was not significantly different from 1.0 ($t_{16} = 0.61, P > 0.50$), indicating that colony volume increases in direct proportion with the number of workers in the nest.

Examination of the ant heads revealed that one of the nests did not belong to *F. pallidefulva* per se, but was enslaved by the dulotic *Polyergus lucidus*. However, as the slave-makers do not contribute to colony maintenance tasks, the nest morphology was indistinguishable of that typical for *F. pallidefulva*.

One of the most salient features of a *F. pallidefulva* nest is the uneven distribution of excavated volume with respect to depth. Though the nests may be as deep as 40 cm, most of the excavated space is concentrated in the first 15 cm or less

below the surface (Fig. 4). To determine whether or not the overall shape of the nest changes as it grows, exponential functions ($depth = b \cdot e^{b \cdot volume}$), which best describe the distribution of volume with respect to depth (Fig. 4), were fitted to each nest. The overall fit of the model to the data was good (average R^2 was around 74%) and the exponential coefficient, which describes the nests' shape, was estimated as -1.3 ± 0.46 . The nest grows without changing the depth-volume relation, as indicated by the lack of correlation between the exponential coefficient and depth ($r = 0.029, P > 0.90$).

Root scarring of the plaster cast decreased with depth ($r = -0.53, p < 0.001$). The large number of roots and frequent chamber mergers (i.e. the dependence of chamber shape on extrinsic factors) in the upper section of a nest made the analysis of individual chambers impractical for the purposes of elucidating excavation rules. The analyses below apply only to chambers in the lower section (depth greater or equal to 7 cm) of the nest.

Chambers tended to be oriented in the direction of the tunnels leading down to them ($r = -0.71, p < 0.001$), suggesting that tunnel direction influences chamber excavation. The average height of chambers (15 ± 1.4 mm) was significantly different from the average diameter of tunnels (13 ± 1.4 mm), indicating that the distinction between them is not arbitrary ($t_{67} = 7.9, p < 0.001$). None of the other variables measured exhibited significant trends.

Excavation

Effects of tunnel orientation on chamber orientation

The orientation of the tunnel greatly affected the outcome of future digging, especially the direction of chamber excavation. Ants forced to dig through skewed conduits continued in the same direction ($\pm 11^\circ, p < 0.001$). Conversely, the

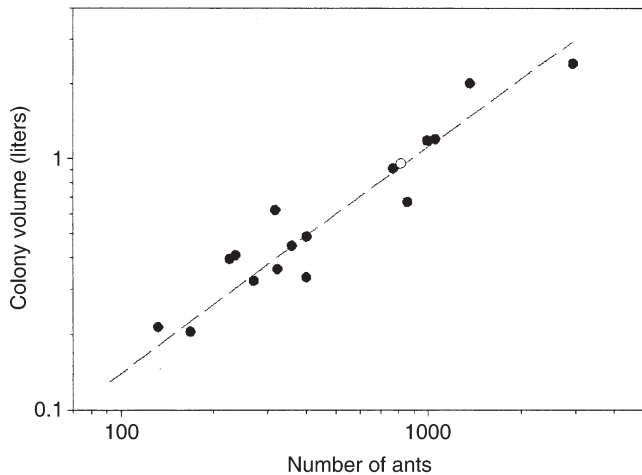


Figure 3. Relationship between nest volume and the number of ants in it ($y = 0.37 + 0.96x, R^2 = 0.87$). The open circle represents the *Polyergus lucidus* colony

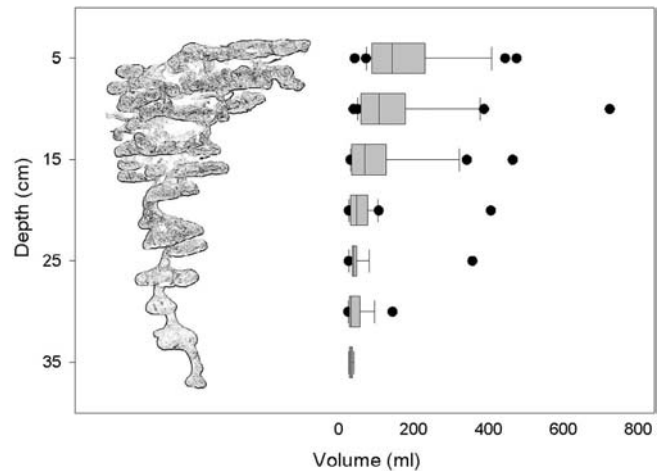


Figure 4. Distribution of nest volume per 5 cm depth interval pooled for all nests. A typical *F. pallidefulva* nest is shown next to the boxplot of volumes. Boxes represent 25th and 75th percentiles, while whiskers stand for 10th and 90th percentiles. Outliers are shown individually (most belong to one large colony)

directions of chambers made by ants digging through a vertical conduit was not significantly different from a uniform distribution ($p > 0.50$). These results are consistent with the correlation between tunnel angle and chamber angle made in plaster casts.

Load size estimation

In three trials involving two colonies the mean load size was estimated to be 2.26 ± 0.18 mg (or 1.56 ± 0.37 μ l, using 1.45 mg/ μ l for the density of sand). The average live weight of a worker was 7.54 ± 1.61 mg. Thus, a worker carries approximately 30% of her body weight in sand during excavation.

Digging time

Though the amount of time it took an individual worker to remove a load of sand varied considerably, digging at greater depths took more time on average. As the worker travels twice the distance of the conduit (descending and ascending), the regression's slope represents half the average climbing speed of a worker (3.1 ± 0.54 cm/s). The intercept corresponds to a worker's mean loading time (15 ± 3.0 s).

Effect of environmental factors on digging

While higher temperatures resulted in greater amounts of excavated sand being excavated ($F_{1,31} = 14.1$, $p < 0.01$), there was no detectable effect of slightly elevated (0.4 percent) CO₂ concentration ($F_{1,31} = 2.55$, $p > 0.10$). However, the percent water in the excavated sand was significantly correlated with the amount of sand removed by the ants ($r = 0.33$, $p < 0.05$). The correlation between the moisture content of sand and the amount of sand removed was not linked to the drying out of sand at high temperatures, as temperature was not correlated with percent sand moisture content ($F_{1,31} = 0.98$, $P > 0.30$). Consequently, it appears that the amount of sand excavated by the ants was linked to both soil temperature and soil moisture content.

Cost of excavating nests

The amount of work required for the excavation of the nest was estimated using the distribution of volume with respect to depth and a worker's average weight and load size. Specifically, the energetic expenditure was calculated from the number of times a worker plus its load would raise to the surface and descend unladen from every 5 cm interval of nest depth. The amount of work required to remove all the soil from a nest in the field, ranged from 130 J to 8,800 J (median 790 J). Given the digging abilities of an 'average' ant in the lab, the number of trips made by the ants translates into anywhere from 10,000 to 460,000 (median 81,000) ant-h of excavation at 28°C. If all workers participate equally, each ant should contribute 158 ± 66 h of labor to nest excavation. In other words, de novo creation of a nest should take about a week, regardless of colony size. In practice, this time may be considerably longer, as all ants will not work simultaneously.

Discussion

The depth of a colony was not correlated with the number of workers in the nest, suggesting that the depth is either limited by the high water table in the area where the study was conducted or that it was at an optimum with respect to some environmental factors. Within these constraints colonies grew by adding more chambers, which were located along a shaft. Nests grew by installing entirely new shafts alongside previously existing ones. Thus, sections of tunnel with associated chambers appear to be modular units of *F. pallidefulva* nest architecture.

Shape, size and distribution of chambers vary greatly among species, suggesting that these differences may be adaptive specializations. However, until these features are quantified and compared across a range of species it is difficult even to speculate about any functions this architectural diversity may have. On the other hand, total nest volume may regulate the density of ants. Ant density may be crucially important in colony function, as increased ant densities have been found to decrease brood rearing efficiency (Brian, 1953). The agreement between the number *F. pallidefulva* workers in the nest and the nest's volume was close over the 32-fold range in colony size, indicating that the density of ants remains unchanged as a result of colony growth (Fig. 3). Both the present study and Tschinkel's (1999) work on harvester ants have shown that the distribution of volume with respect to depth is independent of nest size. Furthermore Tschinkel (1999) found that the number of workers at a given depth increases proportionally with nest volume. These findings further support the notion that nests volumes are carefully regulated at all nest sizes and may play a role in enforcing social organization.

The cost of nest excavation for a colony depend on how often a colony it moves, which is about once or twice a year in most ants (Hölldobler and Wilson, 1990). Assuming that the energy intake requirements of *F. pallidefulva* per gram colony mass are the same as those estimated for non-nest building lab colonies of fire ants *Solenopsis invicta* (Macom and Porter, 1995), and that a colony moves twice a year, we may calculate the percentage of energy intake that is allocated to nest construction. In order to do this, we divide the energy spent on nest excavation by the total energy expenditure (digging cost and all other costs, as estimated by Macom and Porter (1995)), arriving at ~20%. Similarly, given that *F. pallidefulva* in Florida is active during roughly eight months (from mid-April to the mid-November) of the year (ASM, pers. obs.) we may calculate that colonies spend at least 6% of their active time excavating their nest. However, as the time estimate is based on the rather unrealistic assumption that all workers dig, the actual length of excavation may be considerably longer. Note that the time spent excavating not only bears the direct costs of excavation, but also possible opportunity costs of committing workers to nest improvement rather than to food acquisition.

It is conceivable that the lab experiments underestimated the ability of the ants to dig in the field. Some sources of error include the possibility of bias produced by workers climbing on an unnatural substrate (mosquito netting) during

the timing experiments, the pooling of foragers and corpulents during digging trials and the chance that workers' motivation to dig may be altered in the lab. On the other hand, our estimates assume completely linear, non-winding tunnels, neglect the possibility of traffic jams along the narrow passageways, and assume that digging takes place at a fairly high soil temperature. In other words, though by no means exact, our estimates nonetheless provide an approximate figure of nest excavation costs.

If the corpulents and foragers differ in digging ability, the cost to the colony may conceivably be reduced by employing the group most suited to the task. Chen (1937a, b) reported that nest excavation was initiated by 'leaders', who were especially suited to the task. In general, the propensity of a worker to dig may be a complicated function of many variables, including a dependence on prior experience. Evesham (1992) found a strong negative correlation between the time *Myrmica rubra* workers spend in the lab without soil and the amount of soil they excavated during an experiment. Similarly, we have noticed that colonies of *F. pallidefulva* kept in lab nests for extended periods of time were markedly harder to induce to dig and appeared to become less efficient excavators. Of course, both these results could be explained by some potentially deleterious effect of lab life on the ants (for which, however, we have no evidence). Nonetheless, it would be interesting to see whether or not digging specialists exist as a separate caste, and, if so, how they differentiate from ordinary workers during their development.

Several hypotheses may be proposed for the top-heaviness of a *F. pallidefulva* nest. First, as upper layers of the soil remain warmer at certain times of the day, the temperature gradient may cause unequal rates of digging in the nest with more soil being removed in the warm upper section. Second, the high concentration of roots in the upper soil regions may provide structural support for the chambers, allowing the ants to build large chambers without risking cave-ins. Third, sand from the top regions may simply be closer to carry to the surface, reducing the cost of nest excavation. These hypotheses cannot be distinguished using data from this study, but are certainly worth future investigation. As top-heaviness is a feature of many, if not all, underground ant nests it should surely receive more attention.

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