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Ant (Formica Pallidefulva) Nest Architecture: Structure and Rules of Excavation

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ANT (*FORMICA PALLIDEFULVA*) NEST ARCHITECTURE:
STRUCTURE AND RULES OF EXCAVATION

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To my grandfather, Vladimir Ivanovich Mikheyev, whose love of bees and nature inspired me to pursue this path.
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ABSTRACT

The nest architecture of underground ant nests was studied in *Formica pallidefulva*. These ants build shallow (30-45 cm deep) nests, which consisted of more or less vertical shafts that bear chambers. Shafts appeared to be modular units of nest growth; nests were enlarged by adding more shafts or extending previously existing ones. The nests were top-heavy, their volume declining exponentially with depth. The total volume of the nest was strongly correlated with the number of worker occupying the nest. Several rules and templates that may be 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 was related to the soil temperature and the moisture content of soil. The amount of time and energy required to construct a typical nest were estimated using digging ability parameters estimated in the lab. It was found that if a colony was to move twice a year, it would expend 21% of its energy intake and 6% of its worker time on nest excavation.
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 where an ant species makes its nest influences many aspects of the species’ 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 make do with almost any crevice and became pandemic after centuries of traveling inside 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, perhaps of some adaptive value to the ants (e.g., (Cole, 1994)).

Aside from the obvious importance of nests to the ants themselves, they also play a role distributing nutrients throughout the environment. Many species of ants make considerable contribution to the soil turnover in the ecosystem (Kalule-Sabiti, 1980; Wang et al., 1995; Cammeraat et al., 2002). Additionally, ant nests contain elevated levels of organic materials, which become available to plants or other animals after the ants move (Lockaby and Adams, 1985; Carlson and Whitford, 1991; Eldridge and Myers, 1998). The enormous mounds of leaf cutters, such as *Atta cephalotes*, create forest clearings when active and act as centers for plant recruitment when extinct (Garrettson et al., 1998).

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); Tschinkel (1999); Cassill et al. (2002); Mikheyev, submitted).

All the underground nests described consist of networks of chambers and tunnels. Chambers typically contain brood and workers, while tunnels provide connections between them. Except for fungus gardening ants, which have roughly spherical chambers (Wheeler, 1907), the chambers of most ants are vertically flattened. In most cases chambers are vertically stratified and may have 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 over four meters 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 culmination of the 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) attempted to reconstruct species-specific patterns based on the digging patterns on solitary workers. 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 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* and *Formica polyctena* workers position themselves within a nest in response to temperature gradients (Ceusters, 1986), while workers of the desert ant *Messor ebenius* 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 carefully describe and measure prominent features of the architecture belonging to one ant species. Then, we looked at some of the rules ants may use to create such a nest and environmental factors that may act as templates guiding construction. Finally, we estimated the costs of *de novo* nest excavation both in terms of time and energy.

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

Nest Architecture

The study site was located in the Apalachicola National Forest, located approximately fifteen km southwest of Tallahassee, FL. The vegetation consisted of longleaf pine (*Pinus pallustris*) as well as a ground cover of gallberry (*Ilex coriacea* and *Ilex glabra*) and runner oak (*Quercus sp*). Between 1\textsuperscript{st} and 4\textsuperscript{th} April 2001 twenty-five colonies of *F. pallidefulva* were cast in dental plaster at daybreak, before the onset of foraging. Dental plaster was dissolved 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 sample 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 it was not always possible to assemble the cast in its entirety due to missing pieces, all ‘intact’ casts were >90\% complete by weight. For descriptive purposes several operational definitions were introduced: (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. Chambers were subdivided into two types: lateral chambers, which were tangent to a length of tunnel, and apical chambers, which caused a discontinuity in a tunnel (see Figure 1). The distinction between chamber types comes from the supposition that apical chambers represent points where the digging of the tunnel was interrupted, possibly during separate bouts of excavation. The stretch of shaft between two apical chambers, representing the amount excavated in the supposed bout of excavation was named a sub-shaft.

The plaster casts were weighed; the number of chambers (both types) 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 around 1.3 g/cm$^3$ 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 provided a tool for exploring of volume per unit depth. Consequently, most analyses of the relationship between nest depth and volume were conducted on the 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 direction (the bisector of the angle that spans a chamber), 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.

Plaster casts of the nests were broken down, placed in mesh bags and dissolved in a seawater current. 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.

‘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 haphazardly from one of the laboratory colonies.

**Effects of Tunnel Orientation on Chamber Orientation**

Workers were induced to dig under two treatments: a vertical 2 cm conduit and a \(2\sqrt{2}\) cm long (2 cm high) conduit skewed at a 45° angle. A nail was pushed 3 cm into the conduit to make sure that all digging took place in the PVC digging column below the conduit. In other words, while the direction of motion was provided by the conduit, the actual direction of excavation was not constrained. After six hours of digging the nest was exhumed and the depth and direction of the chamber was recorded.

**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 round 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 and a replacement was introduced into the arena 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 CO$_2$ on the ants’ ability to dig was measured in a CGA/Precision Scientific water jacketed CO$_2$ incubator. Workers from one large colony were used throughout the CO$_2$ 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 were permitted to dig for six hours at a set temperature and ambient CO$_2$ 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 Nest Architecture**

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 were estimated with the calibration curves.
provided in 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 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.

Finally, the estimates of provide an estimate of an ant’s power output in watts
(work/time).

**Statistical Analysis**

Data were analyzed by standard techniques using or 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. All means are given ± one standard
deviation for normally distributed data. Otherwise, the minimum, maximum and median
values are provided.
RESULTS

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 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.

Nest Architecture

There were no significant differences among the sampling sites with respect to nest volume (P>0.10, F$_{4,16}$=2.2) or nest depth (P>0.70, F$_{4,16}$=0.46). Given the lack of significant differences and the spatial proximity of the sampling sites, nest data were pooled. The distribution of the 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. Colony statistics are presented in Table I. Curiously, while there is no strong relationship between nest depth and the number of ants in a colony (P>0.05, N=17), the number of ants does correlate with the number of shafts present in the nest (r=0.60, P<0.02, Figure 3). Similarly, the
number of chambers increases with the number of ants in the nest ($r=0.81$, $P<0.001$, Figure 4). The percent of apical chambers (and thus sub-shafts) also increases with the size of the worker population ($r=0.63$, $P<0.01$, Figure 5).

The volume of a nest was closely related to colony size, as can be seen in Figure 6. The slope of the regression of nest volume on worker number is not significantly different from 1.0 ($t_{16}=0.61$, $P>0.50$), indicating that colony volume increases proportionately 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 structural 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 (Figure 7). The negative correlation between volume per depth and depth itself is significant ($r=-0.41$, $p<0.001$, $N=98$). This increase in volume is not simply a result of the ants excavating more chambers.

To determine whether or not the overall shape of the nest changes as it grows, exponential functions ($\text{depth} = b*\text{e}^{b*\text{volume}}$), which best describe the distribution of volume with respect to depth (Figure 7), 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 was estimated around $-1.3\pm0.46$. The coefficient was not correlated with total nest volume ($r=0.029$, $P>0.90$), indicating that the nest grows without changing shape.
Qualitatively, the topmost area of the nest appeared rather different from the structures below, with less definite gradations between chambers and tunnels. However, the heights of the topmost chambers is not significantly different from the chambers found below (t=1.78, N=16, P>0.09), suggesting that the mechanisms involved in the excavation of these areas of the nest are not necessarily different. The shape of the nest may be influenced by the presence of roots, which decrease in abundance deeper into the soil. Root scarring of the plaster cast varied with nest volume at a given depth (r=0.53, p<0.001, N=98).

The large number of roots and frequent chamber mergers made the analysis of individual chambers impossible in the upper section of a nest. The analyses below involve only chambers in the lower section (depth greater or equal to 7 cm) of the nest.

Orientation of the chambers was correlated with the horizontal component of direction of the tunnels leading down to them (r=0.711, p<0.001, N=68). 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=7.9, N=68, P<0.001). There was no correlation between depth, tunnel angle, chamber area, or chamber height (P>0.05, N=98). Tunnel width was weakly negatively correlated with depth (r=-0.29, P<0.02).

Excavation

Effects or Tunnel Orientation on Chamber Orientation

The angle of the tunnel greatly affected the outcome of future digging, especially the direction of chamber excavation. Figure 8 shows the direction of the chambers excavated, given either the eastward (90°) skew of the conduit (treatment) or a vertical conduit
While the directions of chambers produced by ants in the vertical conduit group were uniformly distributed (P>0.50), the orientation of the skewed conduit group’s chambers was indistinguishable from that of the tunnel (95±11°). The control group also dug deeper (P>0.05, t=2.8, N=6).

**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 µl, using 1.45 mg/µl 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. The slope of the regression represents half the average climbing speed of a worker (3.1±0.54 cm/s). The intercept corresponds to the mean loading time for a worker (15±3.0 s).

**The Effect of Environmental Factors on Digging**

While higher temperatures resulted in greater amounts of sand being excavated (P<0.002), there was no detectable effect of slightly elevated (0.4 percent) CO₂ concentration (P>0.10). However, the percent water in the excavated sand was significantly correlated with the amount of sand removed by the ants (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 (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.

**Costs of Nest Architecture**

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 amount of work was assumed to equal the number of times a worker plus its load would have to be raised to the surface from every 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-hours 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. During the course of excavation, an ant spends energy at the rate of 12±7.3 milliwatts.
DISCUSSION

The agreement between the number of ants in the nest and the volume of the structure they excavate was close over the entire 32-fold range in colony size (Figure 6). 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. Short shafts appear to have been occasionally extended, as evidenced by the increased percentage of apical chambers (interrupted shafts) in large colonies. Furthermore, 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 to even 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 cause of brood rearing inefficiency, examined in *M. rubra*, appears to
be a result of all the ants’ general tendency to put brood into piles and the tendency of nurse ants to separate and service the brood (Brian 1956). As the number of ants increases, the tendency to pile brood becomes too strong to ensure that it gets properly fed. However, in *F. pallidefulva* the increase in the size of the nest was proportional to the increase in the number of ants inhabiting it – densities of ants appear to be unchanged as a result of colony growth. Thus, we would not expect brood rearing efficiency to decrease with colony size. A similar pattern has been described for the thatched nest of fungus gardening ant *Acromyrmex coronatus*, where the density of workers remained unchanged across the range of colony sizes sampled (Mikheyev, submitted). However, the case of *A. coronatus* may be rather unusual, as changes in worker density affect not just the nature of the ant-brood interactions but also the relations between ants and their fungal symbiont, which occupies most of the nest structure. Though an isometric relationship between total chamber area and worker number appears to be the case in the winter-active ant *Prenolepis imparis*, the relatively small number of colonies excavated by Tschinkel (1987) does not permit us sufficient power to conclusively resolve the issue. However, in the harvester ant *Pogonomyrmex badius* total chamber area per worker significantly decreases with colony size (Tschinkel, unpublished). Harvester ants have chambers that are devoted to seed storage as well as brood maintenance, so changes in worker number do not necessarily reflect changes in caste or age composition. Thus, the mere lack of an isometric relationship in a given species does not necessarily imply that these ants are less efficient brood rearers at larger colony sizes. Nonetheless, the fact that some ants adjust the size of their nest with such precision implies the importance of maintaining a constant ant density.
Somewhat complicating matters, is the fact that worker density is non-constant at the various nest strata (Tschinkel, 1987). However, both the present study and Tschinkel (1999) found that, the volumes and at a given depth increase proportionally. 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.

Unfortunately, there are few experimental data on the effects of nest architecture on brood rearing. Brian (1956) found Myrmica rubra placed into partitioned nests had a constant ratio of brood tenders to brood, regardless of worker densities involved. However, he did not report data on the efficiency of brood rearing in partitioned vs. non-partitioned nests. Cassill et al. (2002) found no differences in the efficiency of brood rearing by fire ant Solenopsis invicta colony fragments at varying worker densities over the course of one brood cycle. Such an experiment should probably be repeated with queenright colonies and carried through for a longer period of time. In any case, some work is required to reconcile the findings of Cassill et al. (2002) with previous data suggesting that small S. invicta groups are more efficient at rearing brood than large groups (Porter and Tschinkel, 1985).

The cost of next excavation for a colony depends on how often it moves, which is about once or twice a year in most ants (Hölldobler and Wilson, 1990). F. pallidefulva in Florida is active during roughly eight months (from mid-April to the mid-November) of the year (personal observations). Assuming that the energy intake requirements of F. pallidefulva per gram colony mass are the same as those estimated for S. 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, namely 22%. Similarly, we may calculate that colonies spend about 6% of their active time excavating their nest. Note that the time spent excavating not only bears the direct costs of excavation, but also possible hidden 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 should nonetheless a ballpark 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 cast, and, if so, how they differentiate from ordinary workers during their development.

The distributed model of colony construction developed by Emerson (1938) requires a framework for the organization of workers. Grassé (1959) introduced the concept of stigmergy to model the de-centralized dynamics of social organization of nest construction in termites. Stigmergy is defined as the cascade of self-modifying activity where the actions of one worker, such as the alteration of a part of the nest, trigger a behavioral response in another worker. A likely example of stigmergy in *F. pallidefulva* is the ‘inertia’ that causes the ants to excavate chambers in the same direction as the tunnels leading up to them. Stigmergy does not assume that the workers act as a group; conceivably the whole structure could be completed by one worker. However, stigmergy is merely a mechanism for mediating worker interactions and is not sufficient to regulate collective building (Theraulaz et al., 1998). Specifically, it lacks a mechanism for beginning and terminating the activities of a group of organisms. Yet, the possible existence of ‘leaders’ (Chen, 1937a, b) implies that ants may communicate the progress and course of excavation to each other. Such communication becomes necessary for tasks as simple as the excavation of a particular chamber in a nest. If there are mechanisms for (a) positive and (b) negative amplification of collective digging, then, given (c) the de-centralized activities of workers, nest excavation fits the three-part definition of a self-organized system as defined by Bonabeau (1998). Self-organization together with
stigmergy provides a powerful and efficient framework for constructing a nest (Theraulaz et al., 1998), especially together with templates such as temperature and soil moisture gradients.

Before we may employ a self-organization paradigm for the excavation of ant nests, the presence of communication among digging workers must be confirmed. There is good evidence that rescue digging of entombed workers involves some form of chemical communication (Blum and Warter, 1966; McGurk et al., 1966; Hangartner, 1969) or possibly stridulation, which is also used by ants to loosen soil (Spangler, 1974). Also, fire ants are able to recognize soil from their own nest and dig in it preferentially (Hubbard, 1974). However, a mechanism by which digging could be amplified or attenuated is not yet clear. Mechanistic studies addressing questions of nest volume regulation and communication among excavating workers are important and promising areas for future research.

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 yield testable predictions, which would be worthwhile to test in the future. As top-heaviness is a feature of many, if not all, underground ant nests it should surely receive more attention.
Table I. Effects of CO$_2$ concentration and temperature on the amount of sand excavated

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Seq SS</th>
<th>Adj SS</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>1</td>
<td>1.09482</td>
<td>1.18857</td>
<td>1.18857</td>
<td>14.14</td>
<td>&lt;0.002</td>
</tr>
<tr>
<td>CO$_2$</td>
<td>1</td>
<td>0.03240</td>
<td>0.21482</td>
<td>0.21482</td>
<td>2.55</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>CO$_2$*temperature</td>
<td>1</td>
<td>0.20541</td>
<td>0.20541</td>
<td>0.20541</td>
<td>2.44</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>Error</td>
<td>31</td>
<td>2.60653</td>
<td>2.60653</td>
<td>0.08408</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>34</td>
<td>3.93916</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Apical and lateral chambers. Lateral chambers (A) radiate outward from the tunnel, while apical chambers (B) interrupt the flow of the tunnel.
Figure 2. Shafts. The nest on the left has one shaft, while the one on the right has three.
Figure 3. Shaft number as a function of the number of ants in a nest. The number of shafts increases with the number of ants present.
Figure 4. Chamber number as a function of ant number. Bigger nests tend to have more chambers.
Figure 5. Percent apical chambers as a function of worker population. The number of times tunnels are interrupted by chambers and then started again increases with the size of the colony.
Figure 6. Relationship between nest volume and the number of ants in it. The open circle represents the *Polyergus lucidus* colony.
Figure 7. Distribution of nest volume per 5 cm depth interval. A typical *F. pallidefulva* nest is shown next to the boxplot of volumes. Boxes represent $25^{th}$ and $75^{th}$ percentiles, while whiskers stand for $10^{th}$ and $90^{th}$ percentiles. Outliers are shown individually.
Figure 8. Effects of tunnel orientation on chamber orientation. Skewed tunnels were oriented at 90 degrees (i.e. eastward), while control tunnels were vertical. Radial distance from the center corresponds to the number of the experimental trial.
REFERENCES


Alexander “Sasha” Mikheyev was born in Kalinin, USSR (currently Tver’, Russian Federation). Having spent much of his life traveling between the USA and the USSR, he finally settled in New York, where he attended the Bronx High School of Science and Cornell University. At Cornell, having flirted with chemistry, he fell under the spell of honey bees, which he studied for several years with Tom Seeley. At Tom’s suggestion, he applied to work with Walter Tschinkel at Florida State University. That suggestion directly led to the completion of the present thesis two years later.

Sasha’s life during those two years was best described by his lab mates during a going away ceremony. A piece of paper was passed around and each lab mate, in turn, was to write two lines of text. Only the last line was visible to each writer. The whole process was facilitated by alcohol and the joyful prospect of the lab finally becoming neater after Sasha’s departure. Here is the resultant avant garde composition¹ (the order and names of the authors are not disclosed; punctuation and grammar were unaltered):

Alexander Mikheyev went to FSU more or less by accident, a decision that had profound consequences for the next several years.

Sasha will be prostate to the higher mind,

¹ Please note that the composition does not necessarily reflect the views of Alexander Mikheyev or anyone else who contributed to it.
bent over digging in every 50 states.

50 brilliant ideas

his excitement has been an inspiration to us all.

He could often be found dissecting the genitalia of his poor ant-drone catamites.

This behavior may become pathologic and should probably be monitored.

The man with the yellow hair/ Of the Formica he did care/

With them did he live/ And to them he did give

So he did, the ever mercurial man.

And not far away, just out yonder in the forest where

the Formica and the Pogos roam

Beware of the vicious Trachymyrmex…