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## Testing the effect of a nest architectural feature in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae)

Walter R. TSCHINKEL



### Abstract

When natural fire ant colonies (*Solenopsis invicta*) are sampled over five orders of magnitude of colony size, their production efficiency (new biomass per current biomass) remains constant, whereas in laboratory colonies, it declines. A striking difference between laboratory and natural nests is the subdivision of natural nests into hundreds of small chambers that limit the size of work groups. I tested the effect of nest subdivision on brood-rearing efficiency in laboratory nests with a single chamber or many small chambers of equal total area. Nest subdivision had no significant effect on any measure of brood rearing efficiency or final colony size. Experiments are still needed to test cause-and-effect relationships between specific features of ant nest architecture and specific colony functions. The results are discussed in the context of the superorganism.

**Key words:** Ant biology, ant nest architecture, production efficiency, colony development, brood production, colony growth rate, experimental myrmecology.

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Walter R. Tschinkel, Department of Biological Science, Florida State University, Tallahassee, Florida 32306-4370, USA. E-mail: [tschinkel@bio.fsu.edu](mailto:tschinkel@bio.fsu.edu)

### Introduction

The function of subterranean ant nests as shelter and as a defensible space is obvious, so why does nest architecture vary so much among species? It stands to reason that ants with large colonies and/or large individuals would build large nests, and vice versa, but across species, nests vary not only in size, but in most of their features. Even for ants of similar colony and individual size, nests may differ in any or several features, including the number and size of chambers, spacing between chambers, chamber shape and volume, number and size of connecting shafts and maximum depth (TSCHINKEL 2015). This raises the question, do particular features best serve particular functions, that is, do they affect fitness, or is at least some of this variation neutral with respect to natural selection? Not only do these questions have theoretical importance, but practical as well, for in the research laboratory, ants are usually housed in simple nests that have little or no resemblance to the natural nest that was the colony's original home. What artifacts in colony function this produces is unknown.

Most subterranean ant nests are composed of the same basic units, namely, more or less vertical shafts connecting more or less horizontal chambers (the shish-kebab unit). All of the elements of these units, including nest depth, chamber shape, size and spacing, seem to evolve independently of each other, creating the range of species-typical nests (TSCHINKEL 2015). Some species build nests composed of multiple units packed side-by-side with variable spacing between units. Most conspicuous and extreme among these are the fire ants *Solenopsis invicta* and *S. geminata* whose nests consist of many shish-kebab units packed so close together that many chambers coalesce (TSCHINKEL

2006). Nests are enlarged by adding more chambers and shish-kebab units as well as deepening the nest, so that a large nest contains hundreds of chambers that average about 5 cm<sup>2</sup> in area and hold about 200 ants (CASSILL & al. 2002). As a consequence, the colony is divided into hundreds of small "work groups" with unknown effects on colony functions but radically different than the typical large, single-chamber nests in which they are housed in the laboratory.

The study of nest architecture naturally raises the question of whether particular architectures, or architectural features affect colony functions, that is, whether some architectures are favored by natural selection over others, thus leading to the observed variation between species. Many phenomena in biological studies invoke the concept of "efficiency", and many authors have used this concept in biological explanations of social insect behavior and colony function. Thus, one can also ask whether the particulars of nest architecture promote efficiency. However, the definition of "efficiency" is often vague and varies from author to author. The rigorous physical definition is the unitless ratio of output to input, for example the percent of input energy that is transformed to work or some other form of energy, and the percent that is lost as heat. In social insect biology, "efficiency" is typically actually a rate, for example, new workers per initial worker per week or food collected per unit time. The energetic version of efficiency would require the estimation of kcal of new ants produced per kcal of food eaten (or collected), and this has almost never been done for any social insect (but see OFFENBERG 2011 for an exception).



Fig. 1: The experimental nests. Nests were cast as plates of dental plaster, and the 5 mm deep chambers and tunnels formed with a router. The nests were covered with glass, and dampened by squirting water along their edges. The total chamber area of the two treatments was the same.

Several authors have reported that larger colonies of social insects produce new individuals less efficiently (BRIAN 1956a, b, MICHENER 1964, PORTER & TSCHINKEL 1985, VARGO 1988) (but COLE (1984) found no such decline in *Leptothorax allardycei*). Several pieces of evidence suggest that colony subdivision may have important consequences for production in fire ants. PORTER & TSCHINKEL (1985) found that the larger the number of workers in simple laboratory nests, the less efficient they were at rearing brood. Notably, their smallest and most efficient group (0.75 g or about 750 workers) was still far larger than the average work group in real nests (200). This falling size-related efficiency suggested that large fire ant colonies are less efficient at production than small ones. However, TSCHINKEL (1993) showed that at any one sample time during the year, production efficiency (calculated from the pupa to worker ratio) was independent of colony size over four to five orders of magnitude. Because this finding contradicts the laboratory studies, it begs for an explanation. One of the many glaring differences between colonies in nature and in the laboratory is the extreme subdivision of natural colonies into many small work groups, a condition that remains constant no matter how large the natural colony because mean chamber size remains constant. Could this subdivision into small, efficient groups be the cause of the constant efficiency as the colony grows? I tested this hypothesis in the laboratory because single and multiple chamber nests that partly mimic the subdivision of natural nests are readily constructed.

## Materials and methods

**Collection of colonies:** During the cool season (January - March), colonies bring the brood and queen into the above-ground mound to warm, and can be readily captured there (TSCHINKEL & HOWARD 1978). One to three trowels full of mound soil were spread evenly in the bottom of large photo trays, and a few minutes allowed for the panic to settle down. If the queen was present, she was easily recognized by her larger size and her attractiveness to workers. The queen, along with a few thousand workers and brood from 20 or more nests were returned to the laboratory for experimental setup.

Brood and workers were separated from each other by etherizing colonies until the workers had just stopped moving, then pouring the colony onto construction paper, and as the workers woke up, tipping the brood off the paper. Workers in the process of waking up do not usually pick up brood, but do hang onto the paper. The proportion of larvae, pharate pupae and pupae in the brood was estimated by counting samples. Once brood and workers were separated, each experimental nest was initiated with the queen, 3000 workers, 1500 larvae and 1500 pupae. Numbers were computed from the weights of counted samples, and the total weight of an item.

**Experimental treatments:** Nests were made of rectangular 26 × 20 cm plates of orthodontal plaster about 2 cm thick with two different kinds of 5 mm deep recesses routed into their tops (Fig. 1), constituting the two experimental architectural treatments: (1) a single large chamber with a

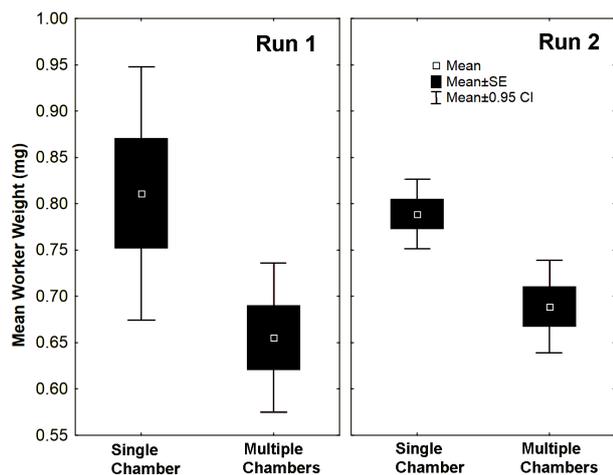


Fig. 2: Worker size by treatment and run. Multiple-chamber nests produced significantly smaller workers in both runs.

diameter of 16.5 cm and an area of 213 cm<sup>2</sup>; or (2) 48 small chambers with a diameter of 2.4 cm totaling the same area. Both types of nests had 5 exits to the foraging arena. The multiple chambers were connected with five 3 cm-wide tunnels running the length of the nest and connecting chambers into three rows with exits at one end of the nest. Chambers near the exits were also cross-connected to simulate the cross-connections in the upper regions of natural nests. Each nest was covered with a 26 by 20 cm plate of glass, which in turn was covered with red cellophane to darken the nest interior for the ants.

Each nest was housed in a 38 by 44 cm photo tray whose sides had been treated with Fluon to prevent escape, and provided with sugar water and water in cotton-plugged test tubes. The same food was provided to both treatments ad libitum in the form of frozen tenebrionid beetle larvae, crickets, Spam, and occasional pieces of meat. The plaster nests were moistened as needed, and were kept in an insect room at about 27.5°C and constant light.

**Treatment switching:** At the end of the first brood cycle (about a month), all nests were disassembled and the number and weight of workers and brood estimated. From these, 3000 workers and 3000 brood were retained to set up the opposite treatment, that is, colonies initially in single-chamber nests were set up in multiple chamber nests, and vice versa. At the end of the second brood cycle, the number and weight of workers and brood were once again estimated, and the experiment terminated.

**Data and analysis:** For each brood cycle and nest treatment, data consisted of the initial number and weight of workers, larvae and pupae, and the final number and weight of each. These basic data produced the number or weight of initial workers that produced the number and weight of new workers and brood at the end of each brood cycle. The most meaningful measure of efficiency is a unitless ratio of input to output, or a factor of increase of number and / or weight. Given the identical starting condition of both treatments, we can assume that the maintenance and work energy did not differ, and dropped out of the equation. Data were analyzed by analysis of variance (ANOVA) using Statistica 13 (Statsoft Inc.). An alpha of 0.05 was applied in all tests.

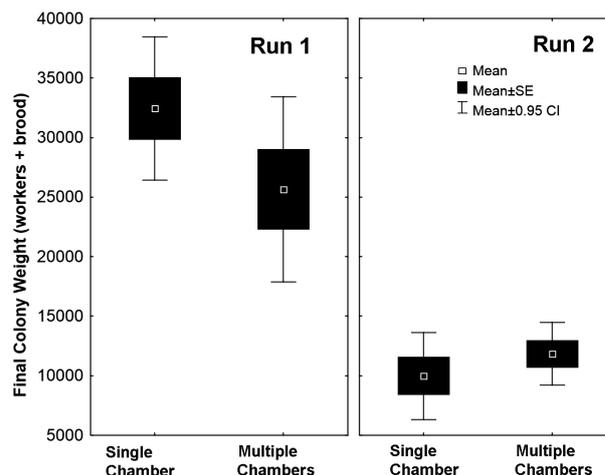


Fig. 3: Final colony weight by treatment and run. Final weight was the sum of live workers and brood, and represented colony production minus worker mortality. Single and multiple chamber treatments were not significantly different, but run 2 was significantly lower than run 1.

## Results

No measure of production or efficiency differed between the two chamber-type treatments (ANOVA, nest type,  $F_{1,33} = 0.022$ ;  $p > 0.05$ ). For example, in the first run, the new biomass produced per initial biomass in single-chamber nests was 4.73, while in multiple-chamber nests it was 4.40. In the second run, these values were 1.03 and 1.53, respectively. This lower performance in the second run than the first run was significant (ANOVA, run;  $F_{1,33} = 32.9$ ;  $p < 0.0001$ ), with means of 4.55 and 1.03. The reason for this poorer performance in the second run is unclear.

The number of new workers (including those still in the form of brood) per initial worker (including those that were pupae at start-up) was also not different between nest treatments ( $F_{1,35} = 0.0014$ ;  $p > 0.05$ ). In run 1, the average was 7.68 (single chamber) and 6.92 (multiple chamber). In run 2, these were 2.75 and 3.45, respectively. Although production seemed higher in the multiple nest treatment, workers produced in these nests in both runs were smaller than those in the single chamber treatment (Fig. 2;  $F_{1,32} = 11.9$ ;  $p < 0.002$ ), so that the new biomass per initial biomass did not differ by nest treatment (see above). As before, there were large differences in biomass production between runs ( $F_{1,35} = 31.8$ ;  $p < 0.0001$ ) for unknown reasons.

The same pattern necessarily pertained to the total weight of colonies at the end of each brood period (Fig. 3); nest treatment showed no difference ( $F_{1,35} = 2.24$ ;  $p > 0.05$ ) while runs showed a large difference ( $F_{1,35} = 51.3$ ;  $p < 0.0001$ ). Queen weight at the end of each run also did not differ by treatment ( $F_{1,35} = 2.25$ ;  $p > 0.05$ ), but did by run, decreasing from 15.8 mg in run 1 to 13.2 mg in run 2 ( $F_{1,32} = 7.39$ ;  $p < 0.01$ ). An earlier version of this experiment in 2016, but at a lower rearing temperature, produced similar results, including the lower production rate by all colonies in the second run, no matter what the treatment (W.R. Tschinkel, unpubl.).

## Discussion

Although the tested nest architectures had no significant effect on brood production efficiency, the experiment was one of the first to test a specific aspect of ant nest architecture on a specific colony function. To the extent that this experiment mimicked the subdivision of field colonies, nest subdivision does not explain the constant size-related efficiency of natural colonies (TSCHINKEL 1993) vs. the declining size-related efficiency of laboratory colonies (PORTER & TSCHINKEL 1985).

This result could have been anticipated by perceptive extension of the results of CASSILL & TSCHINKEL (1995) who found that the number of workers patrolling brood piles for hungry larvae never varied much from a saturation value of 85% coverage. As a result, larvae were assessed for hunger 200 - 800 times / h, but fed only 2 - 50 times / h (depending on their hunger and size). This high excess of assessment rate over feeding rate assured that larvae were reliably fed upon demand, making the production of new ant biomass independent of work group size (at least above a certain worker per larva threshold). This same phenomenon may also explain why the biomass production efficiency of field colonies did not change with colony size (TSCHINKEL 1993), but it conflicts with the observation that production efficiency declined with colony size in the laboratory (PORTER & TSCHINKEL 1985). Given the vagaries of laboratory experimentation, it seems more likely that the laboratory, not the field result, is the artifact. In laboratory nests that are more similar to natural nests (e.g., the cavity nester *Leptothorax allardycei*) the finding that production efficiency was not related to colony size may be less tainted by laboratory artifact (COLE 1984).

Other possible sources of laboratory artifacts come to mind. Husbandry and selection / elimination may bias outcomes, for colonies that do not prosper in the laboratory die or are eliminated from the experiment. In ours, as in all such experiments, the reduction of the captured natural colony to a small size at the beginning of each run risks distorting the division of labor in ways that affect multiple colony functions. At the very least, foragers were probably less represented in the sample, as many were probably afield at the time of capture. Such possibilities must be addressed in future experiments. It is also possible that workers organized themselves into efficient groups even in the single-chamber nests. Given these problems, it is likely that the field assessment of TSCHINKEL (1993) is subject to fewer distortions, and more likely to represent reality.

The most direct test of the nest subdivision hypothesis would have been (and is) to test sexual production by colonies in single and multiple chambered nests, but such tests were of a scale not achievable in my laboratory. Perhaps another laboratory will undertake such experiments.

The multiple chamber treatments did significantly reduce the size of workers, but with respect to biomass production, this effect was compensated by the production of more such smaller workers. The importance of this effect is unclear, but could be related to either chamber size, or nest subdivision. This result could also be seen in the light of a trade-off between worker number and size, a trade-off that is almost universal in founding and incipient ant colonies. Why such a trade-off should be produced by chamber size or nest subdivision is open to speculation. A mechanical explanation is also possible in that the small chambers

reduced access and flow of food, so that larvae grew more slowly and pupated at a smaller size (a trade-off of size and developmental time). In essence, workers in divided nests spread their care and food across more larvae.

The difference between runs could be explained by rearing environment. Brood in the second run had experienced life in the laboratory nests, whereas those in the first run had not. While possible, the larvae had pupated within less than a week of setup, so that for the remaining three weeks of each run, brood had experienced only the treatment conditions. This difference could be controlled for in future experiments by starting with field-collected brood for both runs.

These experiments implicitly view the ant colony as a superorganism (HÖLDOBLER & WILSON 2009), a higher-level entity with functions, regulation and processes whose goal is the production of more superorganisms, and in which the individual ants and their behaviors / physiologies are the moving parts of a larger machine. Seen in this light, the importance of individual level biology is primarily in how it contributes to the emergence of colony level outputs, in particular, to sexual production and founding success. Because ants build species-typical subterranean nests, the obvious question is how do particular architectures serve each species of superorganism. This paper is a first attempt to answer such a question.

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