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Do Florida harvester ant colonies (*Pogonomyrmex badius*) have a nest architecture "plan?"

E. O. Wilson and I recently argued that a renewed emphasis on scientific natural history would reap many benefits (Tschinkel and Wilson 2014), and we are gratified that, inspired by our article, *Ecology* has created this new section called The Scientific Naturalist. A scientific naturalist is, first and foremost, an observer. Something in nature falls pleasantly on a perceptive part of his or her brain, drawing attention to some mysterious or charming phenomenon or creature. Initially, this leads to detailed observations and descriptions, but eventually it may also lead to experiments that test possible causal relationships.

Because I am a myrmecologist, this charm and mystery usually involves ants, and I have poked into their many secrets for decades. One of the abiding ant mysteries is the construction of underground nests. Many species of ants excavate subterranean nests ranging in size from a few cm deep to monumental nests tens of meters in horizontal and vertical extent. When the hollow space of ant nests is filled with a casting material such as dental plaster, molten metal, cement, or wax, the cast reveals the smallest details of the space the ants created underground. Casts of a couple of dozen different ant species' nests have partially bracketed the range of architectures and shown that most ant nests are based on a simple structural "shish-kebab" unit consisting of more or less horizontal, flattened chambers connected by a more or less vertical shaft (Tschinkel 2015). All the features of these units—chamber size, shape, and spacing—evolve independently of one another creating the observed range of species-typical architectures (Tschinkel 2015).

The nest architecture, division of labor and social structure of the Florida harvester ant, *Pogonomyrmex badius* has been described in great detail (Tschinkel 1999, Kwapich and Tschinkel 2013). Having described this species-typical architecture, the challenging question for the scientific naturalist becomes, how do the ants make these nests in the dark, without a leader and without an apparent plan? Or maybe they do have a plan, in the sense that the colony would willingly accept some architectures but not others. The challenge for the inquisitive naturalist is to create a subterranean ant nest that has some resemblance to a real one so that it can be presented with a range of modifications. This is actually less difficult than it sounds. When water is frozen in copper molds in the shapes of the chambers of the Florida harvester ant, *Pogonomyrmex badius* (Fig. 1A), the result is an ice facsimile of the hollow space of a nest chamber (Fig. 1B). Ice chambers can be made in a wide range of shapes, both similar to real chambers or completely unlike them. These ice chambers are then buried in the field at specified depths and connected with a plastic tube. When the ice melts and the tube is withdrawn, the result is a made-to-order subterranean ant nest (Tschinkel 2013). We can then ask what the ants "like," that is, what they will accept as some approximation of the natural architecture they create themselves, and what deviates so much that they do not accept it.

In the natural nest of *P. badius*, the largest, most complex, most closely spaced chambers are always at the top (Tschinkel 2004). With depth, chambers become simpler in outline and spaced farther apart (Appendix S1: Fig. S1A). What if we reversed this chamber order (but not spacing), so that the largest, most complex chamber was at the bottom, and the smallest, simplest at

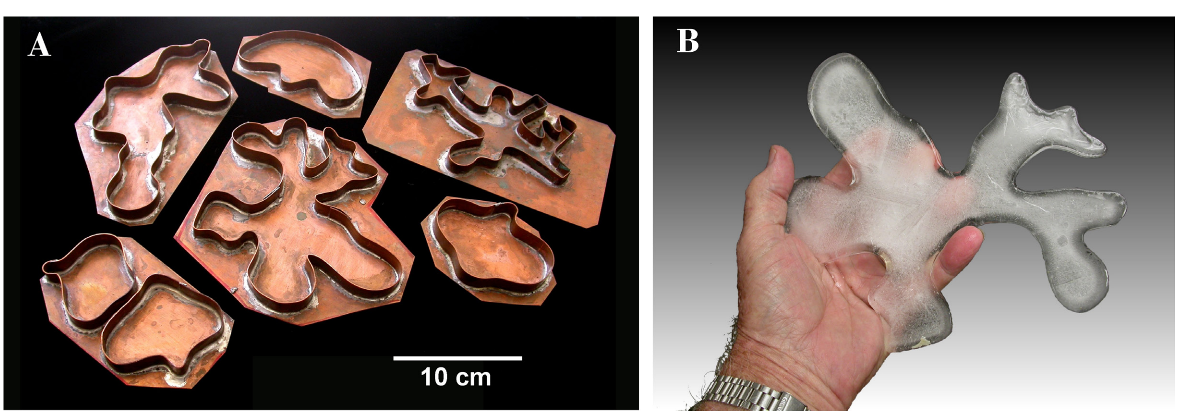

Fig. 1. Chamber molds (A) and ice in the shape of a nest chamber of *Pogonomyrmex badius* (B). Molds are made of soldered copper. Photographs from Tschinkel (2013). [Colour figure can be viewed at wileyonlinelibrary.com]

the top? Both nests will have the same area and the same vertical spacing. What will ant colonies planted in these two variants do?

Appendix S1 shows casts of an ant-made nest (Fig. S1A) along with casts of the two ice nests offered: the normal chamber order (Fig. S1B) and the reversed order (Fig. S1C). The ant colonies were planted in screen-bottom cages so they had no choice but to use the offered nest. After a few days, the nests were dug up, the ants collected and the outlines of the original ice chambers and their modifications by the ants traced. The original ice chambers were recognizable because colored sand had been packed around each at the time of burial.

The results of a single replicate of this experiment are quite striking, and show that the method works. When the natural-shaped chambers were in their normal order, the ants did not modify any of them a great deal (with the exception of enlargement of the deepest chamber; Appendix S1: Fig. S1B). When the chambers were in the reversed order, the ants busily modified all but one chamber (30 cm depth; Appendix S1: Fig. S1C). The most dramatic change was the enlargement of the tiny, oval chamber at 3 cm depth into the complex, branching system of horizontal tunnels that is so conspicuous in natural colonies (Tschinkel 2004; Fig. 2; See Appendix S1 for the full results). But they also enlarged the chambers at 6 and 15 cm because these were smaller than they would be in natural nests. The complex chamber at the bottom of the ice nest also did not meet their expectations, and they changed its size and shape by both filling and excavating (the bottom chamber in natural nests is often larger than those above, but it is always a simple oval in outline). The final outcome in the reversed-order nest was an architecture more similar to the natural nest. In both treatments, the ants added new chambers between the ice chambers, suggesting that I did not provide enough chambers in either one.

What does this outcome tell us about the ants? First, and most obviously, the ants *do* have an "opinion" of what their nest architecture should be. They are particular about both the size and the shape of chambers that they "expect" at each depth, and modify any that deviate too far from this expectation. The total nest area was the same in both ice nests, showing that this measure of the nest is not sufficient for acceptance.

Using variants of such ice nests, it will be possible to test many features of the natural nest architecture in nature. The measure of how closely the variant approximates the ants' "intrinsic plan" will be how much they modify what they were offered, and this modification can be quantified. It is also possible to offer completely unnatural chamber shapes. For example, the ants do not accept chambers that are equilateral triangles, even though the total nest area approximated that of a natural nest. Clearly, the ice-nest method offers a way of asking the ant colony what its "opinion" of "natural" is, opening the way for investigating many details of the mechanism of nest construction.

In a vague, general way, natural chamber shapes already tell us something about how the ants make decisions about where to dig. When workers bunch together side-by-side at the "mine face" for extended periods, the results is an elongated chamber like those near the surface. When their efforts are more dispersed laterally, the result is a more oval or lobed chamber. Whether the ants are responding to each other through social cues or to the perceived shape of the "mine face" (or both) remains to be determined, but it is clear that their behavior changes with depth. When it

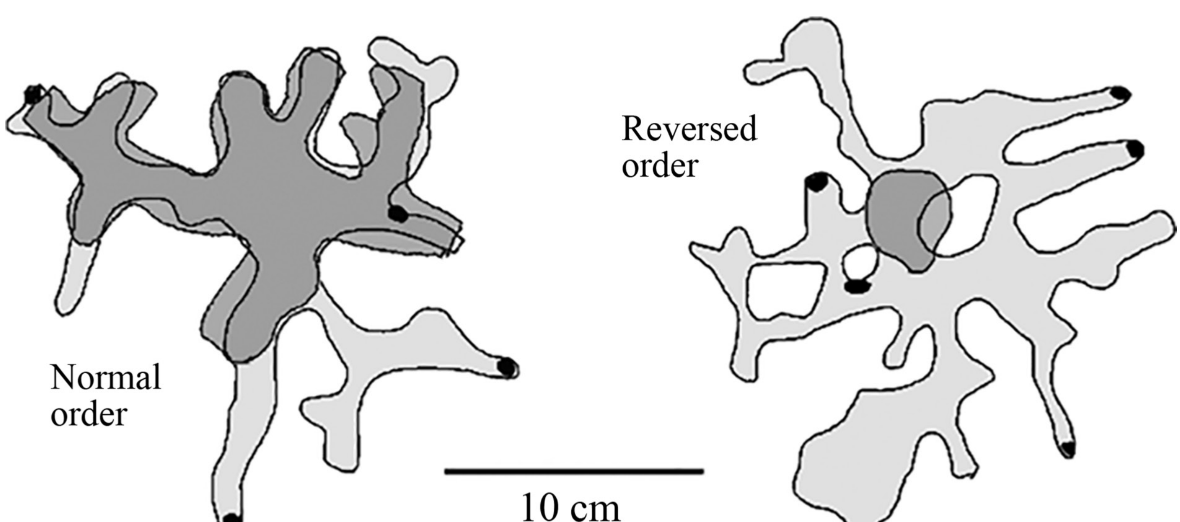

Fig. 2. When offered near surface, simple chambers typical of depths are modified into the complex chambers typical of near-surface (dark shading indicates original; light shading indicates modified).

comes to nest construction, many particulars of this charismatic species are waiting to be revealed.

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