How deep to dig?

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In an intriguing paper in this issue of *Insectes Sociaux*, Römer (2018) and her colleagues ask: How do leaf-cutting ants, when constructing their nest, respond to carbon dioxide levels? Leafcutters in the genus *Acromyrmex* farm fungi, so for these ants maintaining homeostasis involves regulating conditions for both the ants and their crop of fungi.

CO₂ is ubiquitous, benign to most animals at atmospheric concentrations, and, potentially lethal at higher concentrations. Photosynthetic organisms require CO₂ as the basis for building sugars, and heterotrophs release CO₂ into their surroundings as a metabolic product. Unventilated areas, such as nests of social insects, can accumulate levels of CO₂ that may become lethal. In response to the buildup of metabolic by-products in nests—CO₂, water, and heat—many social insects have elaborate architectural systems to enhance air circulation and regulate concentrations of these by-products as well as ensuring a supply of oxygen to support metabolism (Ocko et al. 2017).

Social insect architecture, however, does not result from following a design like an architectural drawing. Instead, each worker makes a decision about its construction work based on information it gathers from its immediate surroundings. The resulting structure is the compounded result of thousands of minute responses. Differences in these simple response patterns among species result in dramatic interspecific variation in nest architectures. The evolution of nest architecture is a fascinating area of study in social insect biology and it is safe to say that we have only the beginning of an understanding of the processes and evolutionary trade-offs that guide nest construction.

CO₂ is a particular problem for tunneling animals, and ants are capable of detecting CO₂ levels in their environment using sensillae on their antennae. This ability, while not unique to ants among the insects, is well developed in

ants, and is an unsurprising feature as they may encounter high CO₂ in subterranean nests. Ants could respond to high CO₂ levels either by avoiding nest construction where CO₂ is elevated or by constructing ventilation turrets that facilitate air exchange.

The question of response to CO₂ concentrations in leaf-cutting ants is complicated by their need to ensure not only their own survival, but also the survival of their fungal garden. High levels of CO₂ inhibit fungal growth, potentially feeding back to diminished colony productivity for the ants. CO₂ levels in soils tend to be higher, by two or three orders of magnitude, than atmospheric concentrations, and increase with depth below the soil surface. It would be reasonable to hypothesize that ants would seek to construct nest chambers at depths that optimize CO₂ concentrations. However, there may be significant trade-offs in terms of soil temperature and moisture that cause ants to choose a compromise nest chamber depth that balances CO₂, temperature and moisture.

Römer et al. (2018) test the excavation behavior of *Acromyrmex lundii* ants at ranges of atmospheric CO₂ concentrations up to 11%. They used two experimental designs; one captured the dependence of digging rate and soil removal rate on CO₂ concentration and the other assessed choices of digging areas based on CO₂ concentration. This species differs from many other Attines in building its nest chambers close to the soil surface.

Digging rate was not affected by CO₂ concentration except for inhibition at the highest level, 11%, a level that would not be expected in soil layers where leafcutters excavate their nests. Soil removal, on the other hand, increased with rising CO₂ levels up to 7%, and then showed an inhibitory decline at 11%. Digging choices suggested a preference for excavation in soils with CO₂ concentrations that favor fungal growth.

These results offer an explanation for this species' nest chambers near the soil surface—that the ants select locations that offer conducive CO₂ growth conditions for their brood and fungi. Other ant species place chambers much deeper in the soil, where they encounter higher CO₂ levels, but more

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constant temperature and humidity and they may respond by building effective ventilation systems.

This paper is exciting because it applies a careful experimental analysis to the trade-offs involved in nest construction. While the behavior of individual ants was not tracked, the group responses to CO₂ help us to understand the dynamics that must be happening at the level of the individual ant. The fact that not all ant species come to the same solution for nest fabrication optimality reflects the subtlety of the evolutionary process and helps us to appreciate the complexity of architecture built on very simple individual rubrics.

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