Self Organization and Associated Behaviors of Nest Building in Ants
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Introduction

Nest creation in ants is an incredibly complex endeavor, involving countless interactions between ants and countless decisions being made. All of this is done seemingly as a single superorganism. There are many subtleties in behavior and the basic biological rules governing such that create this facade and allow for the smooth functioning of the colony.

Self organization in ant societies relies largely on an amplification of the communication occurring among individuals. This is what allows large colonies to seemingly make universal decisions without any one leader. Feedback loops, and minor fluctuations in interactions between nestmates and in environmental features all play a part in the emergence of these self organization patterns. These patterns can appear in a handful of different forms, including abrupt changes throughout the whole colony, timed cycles, waves of communication through a group, and avalanche type events.

Three example of different nest constructions are the harvester ant, the leaf-cutter ant, and the Argentine ant. Harvester ants create nests all with similar overall shapes and proportions. They come out very concise and organized. Leaf-cutter ants seem to just take advantage of whatever environment is immediately in front of them, and thus make very varied nests. They differ in chamber size, number, and placement. One of the few constants is that the chambers containing the fungus grown by the ant colony are always near the surface. Argentine ants' nests are not as extreme as either of the others. The nests are usually created with a similar process, thus resulting in a vaguely similar overall shape.

Digging and excavation behaviors are affected by many factors such as colony size, temperature, age of the workers involved and possibly carbon dioxide levels. Colony size is related to how big the final nest ends up being. In leaf-cutter ants, temperature is a very important factor when
deciding how and where to create a nest because the fungus that they grow has specific temperature needs in order to grow properly. Harvester ants have an arrangement of young workers and older workers that, in conjunction with CO$_2$ levels, affects the final size and shape of the nest.

Individual variable foraging behaviors seem a bit odd at first glance. This means that there doesn't seem to be any set of rules governing each individual decision as is usual, but it almost seems as if individual ants are acting on personal preference, or making errors in collection. When one looks at the fact of a combination of large and small grains creating a stronger wall, it might not fully explain their behaviors, but it makes clearer the benefits of them.

Self Organization Patterns

Ant societies have sets of behavioral rules that dictate interactions between nestmates. These rules allow a colony of ants to act and respond to stimuli seemingly as a single organism. The collective patterns result when the many many interactions that occur between ants amplify the small decisions being made.

Because of this amplification effect, the strength of these patterns strongly depend on colony size. A larger colony offers more opportunities for interactions and specific outcomes than does a small one. For example, a large colony with a high chance of interaction and communication amplification will focus workers on one area that is more preferential as far as foraging. A small colony on the other hand, will spread out workers to multiple sites when foraging since communication cannot be amplified to form a pattern (Detrain, Claire and Jean-Louis Deneubourg. 2006).

In addition to colony size, feedback loops, minor fluctuations and sensitivity to environmental features enable the amplification of communication and thus, the existence of collective patterns. There are both positive feedback loops that activate the release of a signal and negative feedback loops that
repress the release of a signal. The balance of positive and negative feedbacks cause a self-regulation of various situations. Even the tiniest fluctuations in interactions between ants can cause major differences in the global outcomes of situations. For example, when presented with identical sources of food, any small discrepancy of distribution of workers or strength of foraging trails can lead the whole colony to exclusively choose one of the food sources (Detrain, Claire and Jean-Louis Deneubourg. 2006). The sensitivity to environmental features presents a similar situation. Very small changes in environmental factors can slightly affect the interactions between nestmates. But when these small interactions are magnified, they can completely change the final actions of the colony (Detrain, Claire and Jean-Louis Deneubourg. 2006).

There are specific forms of self-organized patterns that are commonly exhibited. The first of these is bifurcation. This is defined as the "abrupt transition of the entire system towards a new stable pattern when a threshold is crossed" (Detrain, Claire and Jean-Louis Deneubourg. 2006). This could be the change in foraging method from disorganized searching to pheromone based searching, or the change from random exploration to a definitive exploratory trail (Detrain, Claire and Jean-Louis Deneubourg. 2006). This is also demonstrated when a colony ceases use of multiple food sources and opts for just one, or when a colony changes from utilizing multiple resting spots to choosing one resting location (Detrain, Claire and Jean-Louis Deneubourg. 2006). This bifurcation is achieved by amplification of communication in the way that if an ant, for example, finally finds food, it will return to the nest and lay a pheromone trail. This trail will attract other foragers who will follow it to the food source and in turn reinforce it with their own pheromones.

Another form of self-organized patterns is synchronization. This refers to the oscillatory processes that occur in living systems that are caused not by external stimuli, but by individuals in the systems. They exist in ant societies and can have periods from a few seconds to weeks long (Detrain, Claire and Jean-Louis Deneubourg. 2006). The daily activity of an ant colony is a perfect example of
This. It's been shown that the factor that initiates the start of work is not external, but the minor movements of the first ant to become active. Longer processes include the alternating of static and nomadic cycles of ant colonies. During the static stage, the queen will lay thousands of eggs. As they hatch, activity levels rise and encourage migration. When the larvae pupate, the static stage begins again. This cycle is caused by any external factors and will occur at the same tempo for years.

Self organized waves are the phenomena in which a wave of chemical or mechanical cues will travel through a colony. Alarm waves have been recorded in Argentine ants (Detrain, Claire and Jean-Louis Deneubourg. 2006). This entails a threshold number of individuals being disrupted and a wave of response initiating and traveling very quickly through the group.

Another form of these patterns is called self organized criticality which refers to "avalanche type events" (Detrain, Claire and Jean-Louis Deneubourg. 2006). In an experiment, Argentine ants collected at the end of a rod to form a "droplet". When the droplet reached around 40 ants, it would drop without any external disturbance.

Architecture and Construction Methods

Nest construction methods and structure vary greatly between harvester ants (Pogonomyrmex badius), leaf-cutting ants (Acromyrmex rugosus rugosus), and Argentine ants (Linepithema humile). One extreme displays very consistent, organized nest structure, while the other extreme shows almost an improvisation in response to immediate environment resulting in much more diverse, variable nests.

Harvester ants' nests consist of distinct shafts and chambers that follow a template shape. A study done by Walter Tschinkel reveals that "the overall 'shape' of the nest changed little during nest growth" meaning that regardless of size, the nests had the same basic structure. The nests generally had a single entrance with an initial shaft that descended at an angle of about 20-30° gradually increasing to
about 45-60° (Tschinkel, Walter R. 2004). The shafts spiral down, creating a helix shape. Off of the branches of spiraled shafts, there are chambers, that begin themselves as horizontal shafts. They are widened gradually until they are roughly circular, then even more until they are multi-lobed. The nests result with an overall top-heavy shape. Most of the chambers and about half of the chamber area occur in the top fourth of the nest (Tschinkel, Walter R. 2004). Both chamber size and frequency decrease as depth increases. Nest size is increased both by adding chambers and deepening the nest, but enlarging the existing chambers contributes most to the increase of the total nest area.

Contrary to the harvester ants, leaf-cutter ants' nests are characterized by "a diversity of irregular chambers and tunnels" (Verza, S. S. et al. 2007). These ants are known to care for and harvest fungus stocks. This activity changes the ants' needs as far as nest construction. The nests studied by S. S. Verza exhibited anywhere from one to 11 entrances, but the number of entrances correlates to the area of the nest mound as well as the number of chambers. Instead of having a template-style distribution of chambers, there was an irregularity to their placement sometimes attributed to the utilization of tree roots, or having chosen to create a nest in a hard to excavate area. Despite this, the chambers were observed to usually be very close to the surface mounds, especially the fungus chambers which were always observed to be so (Verza, S. S. et al. 2007). Besides having the fungus chambers near the surface, the nest components show incredible variability. The chambers and tunnels were both arranged at various angles and varied greatly in size (Verza, S. S. et al. 2007).

Argentine ants display an in-between nest type to harvester ants and leaf-cutter ants. The resulting nests are not as concise and organized as the harvester ants', but there is much more process and pattern to them than the leaf-cutter ants'. The ants begin by digging and deepening small burrows. As the burrows are deepened, the bottoms become flared, or "paddle shaped" (Halley, J. D. et al. 2005). Often times the burrows were created in pairs to be joined later on. The joining of the paddle ends of the burrows creates horizontal tunnels. Branching shafts protrude from these horizontal hallways and
extend far below the rest of the nest. Much like the harvester ants' nests, the Argentine ants' nests result in a top heaviness with a majority of the nest volume falling just beneath the surface (Halley, J. D. et al. 2005).

**Digging and Excavation Behaviors**

The digging and excavation behaviors of ants are affected by many different factors including colony size, temperature, age of the worker ants and possibly levels of carbon dioxide. Despite these numerous factors, scientists have still been able to create models for different excavation situations that accurately predicted the behaviors of the ants.

A model was developed by Jerome Buhl and his crew that accurately demonstrates the relationship between colony size and both the amount and rate of excavation. They found that "when the number of ants varied, the total excavated volume was adjusted in an almost linear way" (Buhl, Jerome et al. 2005). The control of colony size on the rate of excavation is attributed to a double feedback system. The model that they developed to represent the rates of excavation consisted of three main stages. The first two (an exponential growth phase followed by a linear growth phase) demonstrate the positive feedback. This consists of ants rapidly being recruited to dig by sensing the digging pheromone on recently excavated areas. This amplifies the spontaneous acts of excavation that will occur randomly around the nest (Buhl, Jerome et al. 2005). The third stage (a saturation phase where the excavation rate steadily decreases to zero) represents the negative feedback. The negative feedback results from a decreased efficiency of the recruitment process when population reaches the point where the digging pheromone is wearing off before another any can find it and respond to it, meaning that the colony of a certain size will only create a nest of a certain size before excavation stops.
In leaf-cutting ants, soil temperature is another factor that affects digging behaviors. The fungus that leaf-cutting ants cultivate inside their nests is highly reliant on temperature for proper growth (Bollazzi, Martin et al. 2008). Thus, it makes sense that when creating a nest, the ants would concern themselves with the temperature of the soil they're digging in. Bollazzi's study showed that these ants created more subterranean nests in warmer soils and more superficial nests in cooler soils. Mild soils yielded both nest types. The ants tested seemed to have a thermopreference for soils between 20° and 30°C. This thermopreference acts as an orientation cue when beginning to dig. Once digging, workers will also use temperature to guide them in different directions or to stop digging. The ants are constantly seeking out areas of the right temperature, thus if the ant is placed in warm soil, it makes sense that the nest will be deeper because that is where the preferred temperature will occur.

The harvester ants discussed above have a few interesting aspects to their nests. It's been observed that ants at the bottom of the nest tend to be much younger than the experienced workers at the top of the nest. The older ants are able to excavate up to 3 times faster than the younger ants at the bottom. Walter Tschinkel tested the levels of CO₂ in the different layers of the nest. He found that carbon dioxide concentrations were ambient near the surface and increased 5 times near the bottom of the nest. The question is about the fact that the nests have a top heavy shape. It seems as though the difference in age is cause just for the total volume of the nest, while the carbon dioxide gradient is cause for the overall top heavy shape of the nest (Tschinkel, Walter R. 2004).

One example of someone successfully modeling ants' excavation behaviors regardless of seemingly many factors affecting them is Jerome Buhl and his team's model. They described the initiation of new tunnels by two probabilities—whether the tunnels were initiated on the periphery or during branching (Buhl, Jerome et al. 2006). The tunnel growth was based on just a few parameters and was able to successfully mimic the topology observed in the corresponding experiments. They showed that complex characteristics of the components of ant nests emerge from a "simple process of tunnel
growth in a finite space" (Buhl, Jerome et al. 2006).

Foraging Behaviors

When considering foraging behaviors, one needs to look not just at specific factors that may influence them, but also at the context that the behaviors are being considered in. Individual preference and construction cues may play a part in foraging behaviors, but when one considers how the foraged material is being used, more meaning can be derived from the foraging behaviors.

Aleksiev studied the habits of ants foraging for construction material and found that some foragers specialized in carrying big grains of sand and others specialized in carrying small ones. Individual ants were capable of carrying either big or small grains, so foragers who tended to specialize in small grains, did not do so because of morphological constraints (Aleksiev, Antony S. et al. 2007). Instead it seems as though the unique choices among individuals were based on personal measures of cost and benefit (Aleksiev, Antony S. et al. 2007). At a farther distance, ants were more likely to initially choose larger grains of sand, but as the construction of the wall neared an end, they included more and more small grains of sand even at far distances. This indicates that the construction of the wall may be offering cues as to what type of sand to collect. When the fact is considered that the most structurally sound wall is made of about half and half big and small grains, the ants' actions make a bit more sense. While it is unsure what exactly causes certain ants to collect certain sizes of grains at various distances and times, we do know that their actions are beneficial to the construction of their wall.

Other ant species have been observed foraging not only sand grains, but also charcoal, glass, and anthropogenic objects (Smith, C. R. and W. R. Tschinkel. 2005), (Burris, Lucy Ellen). Ant mounds have recently been utilized by archaeologists because of the ants' natural foraging behaviors. There are
small (<5mm) artifacts that archaeologists simply can't find and collect on their own. But by understanding and taking advantage of ants' behaviors to search up to 20 m away from the nest for objects on the scale of millimeters, archaeologists can obtain huge amounts of data that would have previously been impossible (Burris, Lucy Ellen).
References


