# Self-Organization in Social Insects

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Self-organization is a process in which complex patterns or behaviors are produced without direction from an outside or supervising source. This mechanism is observed in a multitude of systems including phase-transitions, oscillating chemical reactions, and the development of fish schools. Self-organization in biological contexts is particularly interesting, as it may be a necessary component of the observed complexity found in organismal behavior and play a vital part in natural selection.

Self-organizing systems in biology are generally composed of many individuals that work collectively to create complex patterns through positive and negative feedback interactions. These patterns are not encoded on the individual level nor are they being built with any knowledge of the global structure, they are instead products of interactions between individuals or between individuals and their local environment. The behavior of many social insects are fitting examples of this process, as the individual insects generally do not have the cognitive power to generate their observed complex structures and activities. For example, the construction of termite mounds, ant walls, honey bee comb patterns and wasp nests, honey bee thermoregulation, army ant swarms, ant corpse-aggregation, and foraging in ants and bees can all be seen as a combination of simple rules on the individual level that produce a global response without any external direction.

The emergent properties of social insects interactions are generally characterized by three properties: complex spatio-temporal patterns from homogenous initial conditions, the existence of multiple stable states that are the consequence of the amplification of random initial heterogeneity, and the presence of bifurcation points, at which a patterns drastically change as a result of small parameter changes (Camazine et al.). Self-organizing systems are strongly dependent on their environment because of their sensitivity to initial conditions and they can simultaneously offer stable patterns that resist perturbations given appropriate parameters. However, they are also capable of variability and drastic change when near a bifurcation point.

This has major implications for the role of self-organization in the evolution of complex patterns. The limited amount of information that can be stored in the genome may be used to produce a plethora of sophisticated behaviors by devoting a relatively small portion of the sequence to simple rules that can yield emergent complexity when aggregated. Thus self-orgnization may be a powerful tool in the optimization of genetic information and in the creation of simple parameters that can be selected for through evolution.

Although self-organization has been proven experimentally in non-biological systems, it is much more difficult to perform similarly conclusive experiments when dealing with organisms such as social insects. It is most likely that the examples presented here are not fully explained by self-organization alone and are instead the product of a synthesis of different mechanisms. However, this does not make self-organization any less attractive as an alternative to other mechanisms for complex patterns such as an organizing leader, blueprints, recipes, and templates.

These alternative hypotheses would often require an unlikely amount of individual complexity. While social insect colonies often have a central leader, such as a single queen, the leader would be unable to efficiently communicate detailed and individual commands to a large group of workers. This problem in communication could be circumvented by individuals already possessing the necessary information to produce complex spatio-temporal patterns in the form of a blueprint that all individuals possess or response or a recipe of step-by-step instructions that direct each worker. Both of these strategies require a large amount of encoded information and recipes make it particularly difficult for an entire community to simultaneously work towards the same global outcome. Another alternative, the template, would provide individuals with the necessary information to produce the pattern. The major drawback to template-guided building is that there is not always a mechanism for template construction. These alternative mechanisms to self-organization are certainly used by other organisms, but it is unlikely that they are the main method of complex pattern formation in social insects. Nevertheless, we will see an example of a possible template-driven behavior in the construction of termite mounds, and it would not be surprising if other patterns were best explained by a combination of mechanisms.

We will now examine biological examples to evaluate models of self-assembly in social insects. A very basic and well supported model of self-assembly explains the formation of ant trails through the use of pheromones. As ants travel between the nest and food sources, they lay a chemical pheromone that attracts other ants. This positive feedback eventually pro-

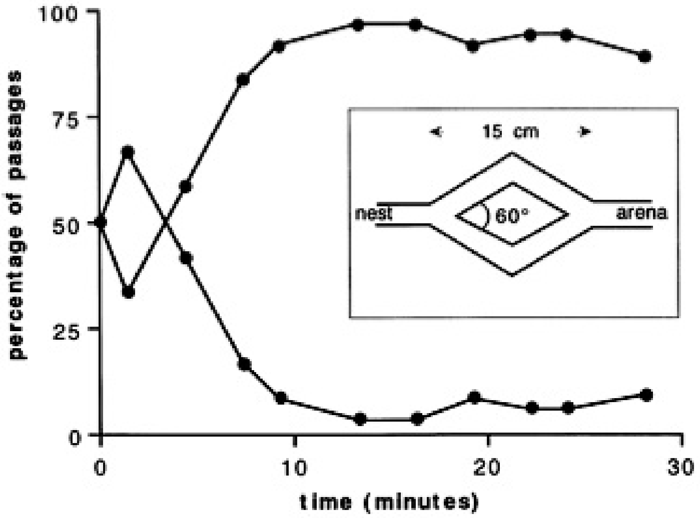

Figure 1: Double-bridge experiment (Deneubourg and Goss 1989) The percentage of ants that chose each of the branches as a function of time. Interestingly, the branch initially favored by random fluctuations was not chosen in the end, as the additional pheromones were not sufficient to produce a run-away positive feedback. The *inset* is a drawing of the experimental setup.

duces an ordered path of ants going to and from the food. The pheromone degrades over time, so once one path has been established, it usually persists, as less traveled paths disappear. This is a simple example that does not reflect the more subtle complexities of the trails used by some species, but clearly illustrates the positive feedback mechanism. The double-bridge experiment done by Deneubourg and Goss in 1989 supports this mechanism with data. They separated a nest of ants from a food source by a bridge with two equally long branches and observed the preferential selection of one bridge over the other. A random heterogeneity in the path selection is amplified and one path is eventually chosen (Figure 1). Negative feedback is manifested through the depletion of food or satiation, which prevent the persistence of trails for unreasonable amounts of time. Overall this example exhibits what appears to be a community decision to favor one path over the other through individual decisions based on local pheromone concentrations and also shows multistability, as either branch could have been a stable out-

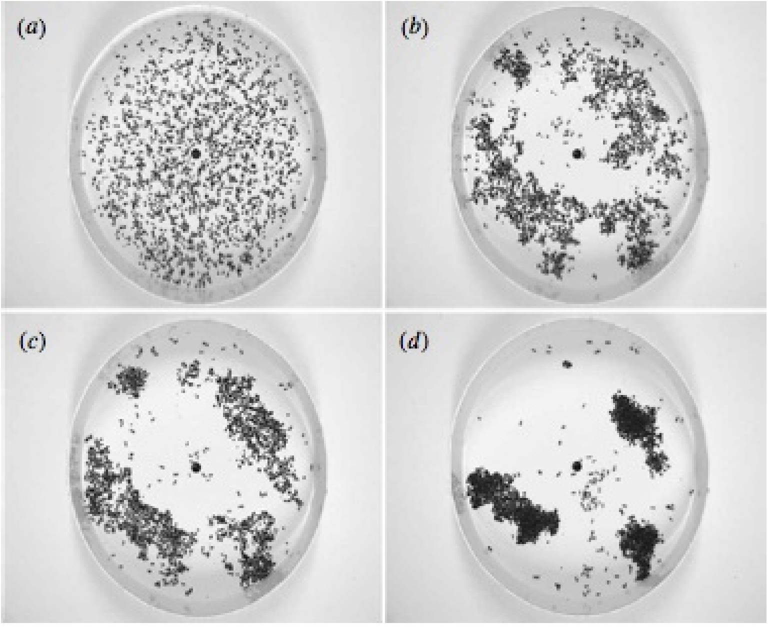

Figure 2: (Theraulaz et al., 2003) Corpse piles formed by the ant *M. sancta* in a 30 cm diameter arena and 1500 corpses. (*a*) Initial conditions, (*b*) after 3 hours, (*c*) 6 hours and (*d*) 36 hours.

come. However, if the branches are of unequal length, the shorter path will be the the only stable state, as the density of pheromones will be necessarily greater. This simple positive feedback mechanism, which amplifies random fluctuations to produce complex patterns will be revisited through the use of analogous examples.

Stigmergy refers to a mechanism that allows one individual's actions to influence the successive actions of other individuals through changes in the local environment. The pheromones used by the ants in the previous example have this quality. An individual ant lays down pheromones, which then influences the subsequent behavior of other ants. The cue is quantitative in nature, as the amount of pheromone present affects the actions of the ants. Likewise, quantitative differences in materials may also act as a stimulus for a favored behavior. For example, ants move ant corpses out of the nest and into clusters because the probability that they will pick up and drop corpses is dependent on the density of corpses around them (Figure 2) (Theralaulaz et al., 2003). As cluster size increases, there is a higher probability that ants will drop corpses and a lower probability that they will pick them up. A set of differential equations, using experimental data, can be made that describes this behavior. Monte Carlo simulations of the model show the formation of corpse clusters similar to those observed in nature and walls of corpses when the density of bodies increases (Figure 3). The importance of the initial density conditions show the multistability generated by the system and the existence of a threshold density necessary for corpse aggregation to occur suggests bifurcation.

A combination of both template and stigmergy mechanisms are used in the construction of the magnificent termite nests of *Macrotermes bellicosus*, which can reach diameters of 30 m and others a height of 6 m (Camazine et al., 2001). These complex structures contain a thick outer wall, brood chambers, a base plate, a royal chamber, fungus gardens, and paths from the nest to foraging sites that are enclosed by walls and a roof (Figure 4).

These termite mounds are extremely complex and have a functional design vital to the survival of the colony. The outer walls protect the colony from anteaters and army ants and also keep the mound very humid relative to the external climate. However, the walls also trap heat, which must be kept in a precise range to allow the growth of the symbiotic fungus the termites cultivate. This fungus is grown on a combination of plant material and feces and makes the plant material easier to digest. The growth of the fungus is necessary for the survival of the nest, and thus the structure of the mound must possess a means to prevent the internal temperature from overheating the fungus. This is accomplished through a series of ducts that act as an air-conditioning system, simultaneously expelling the hot carbon dioxide-rich air and absorbing cooler oxygen-rich air from outside of the mound. Although the construction of this temperature-regulating system is far from understood, the construction of the royal chamber, galleries, arches, and the peripheral paths can be modeled using a combination of template and self-organization mechanisms.

Experiments suggest that the queen termite produces a pheromone that serves as the template for the royal chamber. This template determines the size of the chamber, which is built tightly around the queen. The use of pheromones is important because it provides a mechanism for the growth of the royal chamber in response to the growth of the queen. There are four major positive feedback mechanisms involved in construction of the royal chamber: the attractive cement pheromone that is impregnated into soil pellets before they are used in construction, spatial heterogeneities that may be amplified, the trail pheromone, and the queen pheromone (Bonabeau et al., 1998).

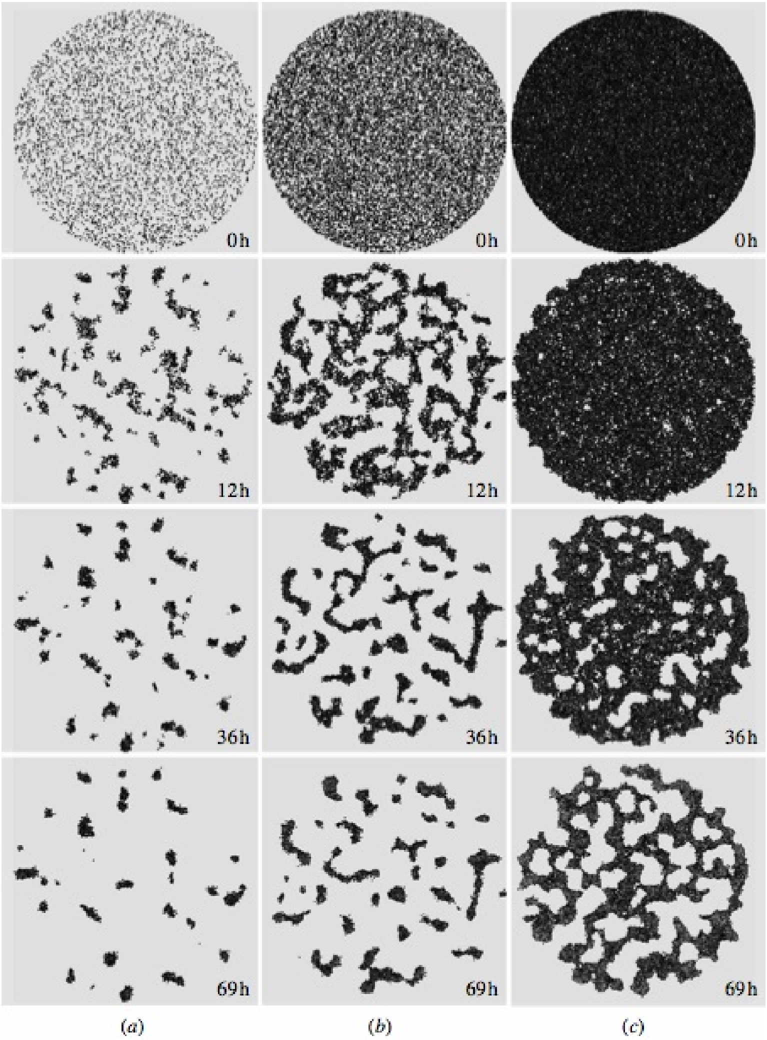

Figure 3: (Theraulaz et al., 2003) Monte Carlo simulations of corpse clustering in a 50 cm diameter arena with a constant ratio of workers/corpses and constant parameter values. The concentration of corpses was (*a*) 5000, (*b*) 20000 and (*c*) 80 000. The patterns after 0 hours, 12 hours, 36 hours, and 69 hours are shown. The lowest initial density of corpses yielded piles, while higher densities formed walls.

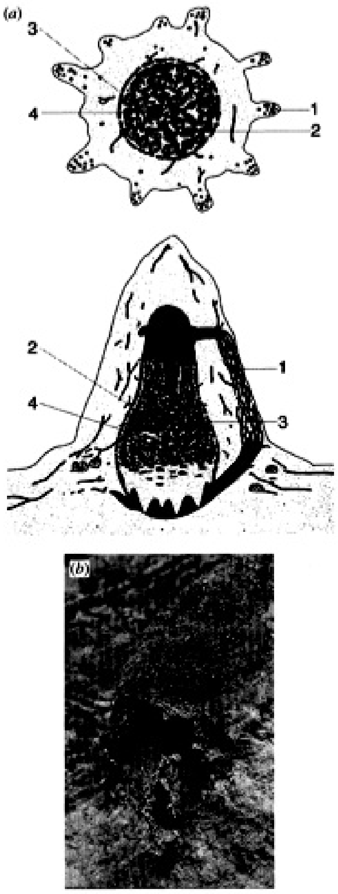

Figure 4: ($a$) (Bonabeau et al, 1998) Cross-section of a *Macrotermes* mound: (1) walls with ventilation ducts; (2) brood chambers; (3) base plate; (4) royal chamber. ($b$) Peripheral path to foraging site.

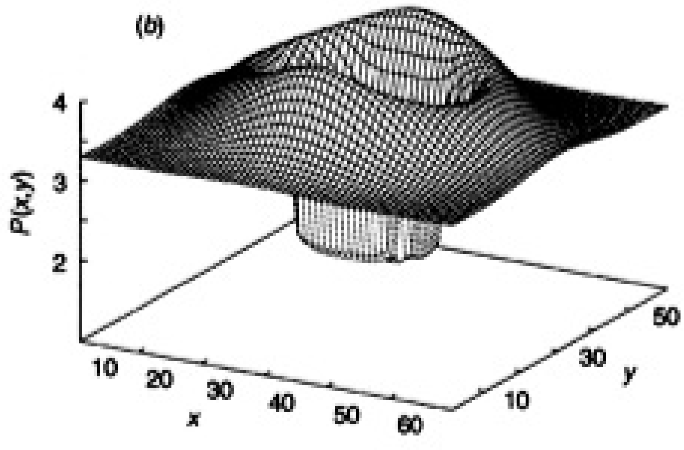

Figure 5: (Bonabeau et al., 1998) Simulated spatial distribution of pellets using equations in Bonabeau et al., 1998 to simulate the royal chamber.

Workers initially place soil pellets at random until a pile reaches a critical size, at which point the cement pheromone will create a positive feedback effect and groups of workers will transform the soil pellets into a pillar or strip. This feedback loop can be inhibited by the decomposition of pheromone, thus if there are not enough workers to maintain pheromone levels, the pillar or strip will not form. The trail pheromone functions similarly to that of ants, and produces a long-term positive feedback. More termites are recruited to aid in the construction as the path becomes more attractive due to frequent traffic. When the chemical template produced by the queen is added to these mechanisms, there is a preferential construction of walls at a certain radius from the queen. The queen pheromone produces a concentration gradient, and the termites have an increased probability of depositing pellets in a certain concentration window. This creates a multilayered positive feedback system that results in the construction of walls a certain distance from the queen. These interactions and many more were made into differential equations were modeled by Bonabeau et al. in 1998 and produced the expected queen chamber (Figure 5).

Additional observed structures can also be modeled when the equations are modified. For instance, when the queen pheromone is removed, the effects of the trail and cement pheromones can produce the enclosed paths going from the nest to food sources. These pathways are surrounded by walls and a roof to protect the termites from predators and the climate as they bring food to the nest (Bonabeau et al, 1998). To model the formation of these paths, the trail pheromone must possess three qualities: it attracts other termites, high concentrations of the pheromone inhibit the deposition of material, and high concentration promote picking up material (Camazine et al., 2001). Thus, as the termites travel along the path there is a greater probability that pellets will be deposited to the sides of the path where there is no inhibition. These initial depositions along the path can then be built upon by the positive feedback mechanism of the cement pheromone. The roofs of the trail are explained by the semi-circle isoconcentration lines that project three-dimensionally from the trail pheromone on the ground, creating a template for arch formation (Camazine et al., 2001). This model also allows for the increase in the width of the paths in response to higher trail pheromone concentrations caused by increased traffic. These models show that some of the architecture of termite mounds can be explained using a combination of template and self-organization mechanisms, and even though they are not necessarily the mechanism used by the termites, they are a plausible explanation of how the termites collectively produce such complex structures. Further experimental data is required to learn more about the possible mechanisms and test the strength of the proposed models.

The self-organization in previous examples centered around quantitative stigmergy, which relies on a simple preference for different amounts of some cue. The construction of some paper wasp nests may be examples of qualitative stigmergy, a process that depends on qualitative differences in the environment to produce emergent complexity. The wasp nests are comprised of layers of hexagonal cells that form three-dimensional structures. Experimental data suggests that the wasps have a higher probability of adding cells in places where it will share three walls with preexisting cells (Figure 6). When this individual building rule is combined with qualitative rules, models can generate wasp nests that are similar in structure to the nests of different species of wasps (Figure 7). These qualitative rules are described by Camazine et al. in *Self-Organization in Biological Systems*:

> When the regulation of the building behavior operates in a strict qualitative stigmergic mode, the only way to build a coherent structure is to use a particular class of algorithms that we call *coordinated algorithms.* In such algorithms, local patterns that result from previous construction and are encountered by individuals moving randomly on the nest structure provide the exclusive cures necessary to direct and coordinate the building

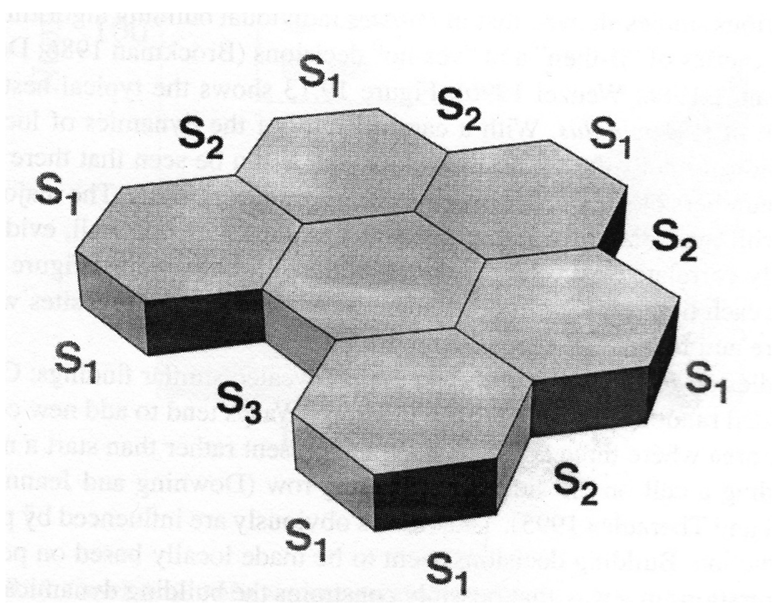

Figure 6: (Camazine et al., 2001) Diagram showing positions having one (S1), two (S2), and three (S3) walls in common with an added cell.

> activities of the group. (440)

Under this model, the nest construction is comprised of a finite number of building stages, each containing specific patterns that stimulate the construction of a new building stage (Figure 8). For further information, see Camazine et al., 2001. It is still unclear how qualitative stigmergy may be used by social insects in self-organizing processes, but it is another example of a mechanism that optimizes sets of simple rules to produce complex structures.

There are a diversity of emergent structures and behaviors that can be explained by self-organization. Although no examples of social insect behavior were examined in this paper, the thermoregulation of bee swarms and other phenomena have been reviewed in Camazine et al., 2001 and other sources. The majority of applications use similar mechanisms as those described in this paper, but may use different variables such as the rate and duration of activities (as in honeybee comb patterns) or temperature (as in bee swarm thermoregulation). Further research must be done to understand how large a role self-organization has in complex pattern formation in social insects and other organisms.

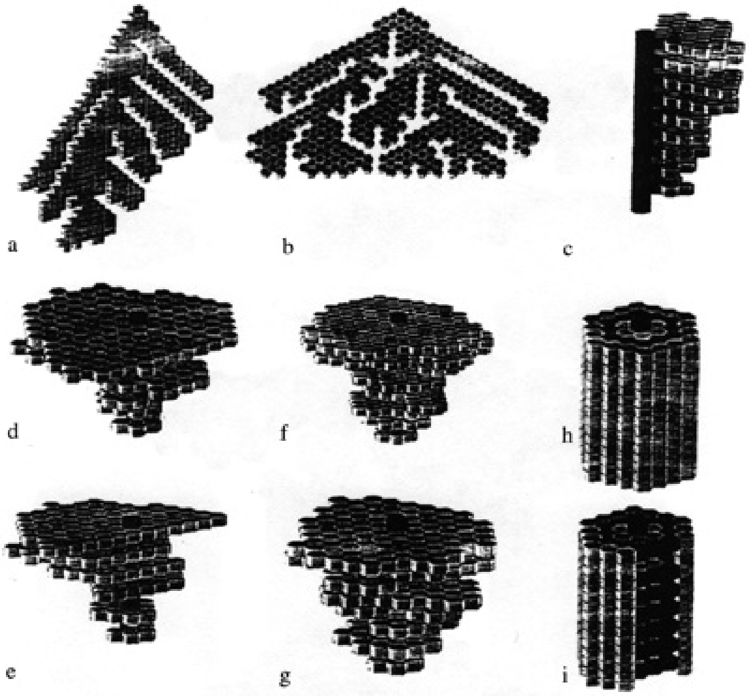

Figure 7: (Camazine et al., 2001) Wasp comb structures generated from coordinated algorithms representing qualitative stigmergy. Real wasp species construct similar combs. (a) *Agelaia*, (b) *Parapolybia*, (c) *Parachartergus*, (d) *Vespa*, (e) same structure as (d) shown in in front section, (f) and (g) *Stelopolybia*, (h) *Chartergus*, (i) same structure as (h) with part of external envelope removed.

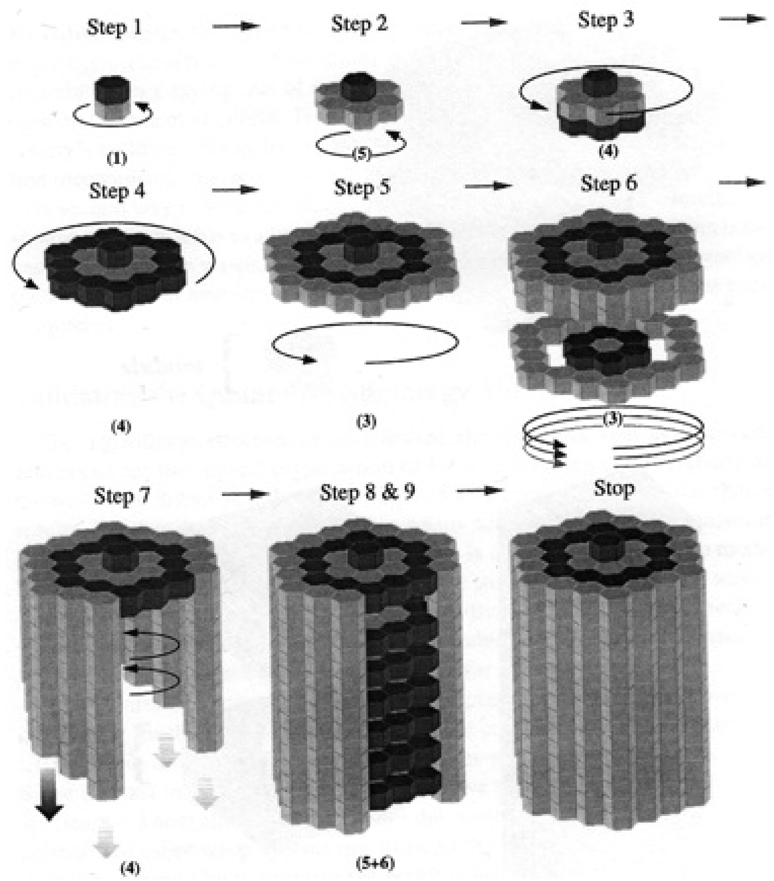

Figure 8: Camazine et al., 2001) The building steps used in the construction of *Chartergus*-like nest. The completion of each step produces the conditions necessary to initiate the next step.

In conclusion, self-organization is a powerful mechanism that can produce complex structures and behaviors. The emergent properties of many biological systems can be explained by individuals following simple rules based on local information. Alternatives to self-organization often require unlikely cognitive ability and genetic coding that can be more simply explained using multiple interactions among individuals that follow simple positive and negative feedback mechanisms. These interactions can often have several stable states and bifurcation points that are sensitive to the environment and specific parameter tuning. Perhaps it is these parameters, not the behavior as a whole, that have been selected over evolutionary time. It is important to remember that self-organization is usually an insufficient explanation for the entire behavior being modeled. We still need of more biological research before we can understand what role self-organization has in emergence and what other interactions may be at play. Nonetheless, self-organization is a fascinating field that may help us explain the intricacy of nature and understand the principles underlying the complexity of biological systems.

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