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Social Insect Colonies as Complex Adaptive Systems

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ABSTRACT

Social insect societies are complex adaptive systems that self-organize within a set of constraints. Although it is important to acknowledge that global order in social insects can arise as a result of internal interactions among insects, it is equally important to include external factors and constraints in the picture, especially as the colony and its environment may influence each other through interactions among internal and external factors. The scope of this remark goes beyond social insects and applies to a wide range of biological systems, including ecosystems.

Key words: social insects; self-organization; complex adaptive systems; template; stigmergy; collective behavior.

INTRODUCTION

A social insect colony functions as an integrated unit that not only possesses the ability to process a large amount of information in a distributed manner, make decisions about how to allocate individuals to various tasks, coordinate the activities of tens or thousands of workers, or undertake enormous construction projects, but also exhibits flexibility and robustness in response to external challenges and internal perturbations (Wilson and Hölldobler 1988). My aims in this report are

1. To parallel Levin's (1998) argument that ecosystems and the biosphere are complex adaptive systems (CAS) to show that social insect colonies are also CAS that self-organize within a set of constraints.
2. To show that the CAS approach has been, and still is, providing important insight into the understanding of social insects.

In attempting to meet these two objectives, I hope to convince the ecological readership of this journal that the lessons learned from applying the CAS approach to the study of social insects are to a large extent applicable to the study of biological systems composed of interacting units, including ecosystems. This special issue gives me the opportunity to review our current understanding of collective behavior in social insects from the CAS perspective and to provide some general guidelines for the identification of the relevant factors that should be, and are not always, taken into account in the CAS approach.

SOCIAL INSECT COLONIES AS COMPLEX ADAPTIVE SYSTEMS

Insect colonies possess the six properties that, according to Arthur and colleagues (1997) and Levin (1998) characterize CAS:

1. *Dispersed interactions*. Social insect colonies are spatially distributed systems.
2. *The absence of a global controller*. Most activities in social insects are regulated not by a central controller but in a decentralized manner via interactions among individuals and between individuals and their environment.
3. *Cross-cutting hierarchical organization*. Many species of social insects have a hierarchical organization that determines the partitioning of reproduction, resources, and tasks.
4. *Continual adaptation to changing environmental conditions*. Social insects have to deal with perpetually changing environmental conditions. Tem-

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perature, humidity, food, predators, or competitors are examples of external factors that require resiliency and robustness.
5. *Perpetual novelty*. The production of new insects by a colony not only influences colony size but also, for example, the pattern of division of labor in the colony. The environment is also a source of novelty that a colony adapts to by changing its organization.
6. *Far-from-equilibrium dynamics*. Social insect colonies are dynamic systems that operate far from equilibrium. This important point will be developed in the section on *self-organization of insects*.

Levin (1998) reduces this list of six properties to three "essential elements":

1. *Individuality of components*. Every insect in a colony is a highly autonomous entity.
2. *Localized interactions among those components*. Direct interactions among individual insects are undoubtedly local. Actions taken by insects are also local. Nonlocal interactions can, however, exist when one individual modifies its environment so that another individual can sense it at a later time. Such interactions are indirect and are local in space but nonlocal in time.
3. *An autonomous process that selects from among those components*. This element is problematic when applied to social insects because selection acts at several levels. Individual-level selection depends on colony-level performance. There is a case, however, in which the local interactions among insects lead to the "selection" of one of the insects: the winner of hierarchical interactions becomes the principal egg layer of the colony in primitively eusocial species.

Finally, Levin (1998), quoting Holland (1995), cites four basic properties of CAS:

1. *Aggregation*. A social insect colony is organized into different groups of individuals that perform different tasks according to their age, morphology, or genotype, or according to chance events.
2. *Nonlinearity*. Interactions among insects result in nonlinear responses and, sometimes, snowball effects. This point is described at length in the section on *self-organization of insects*.
3. *Diversity*. Most social insect colonies are characterized by genetic diversity because the queen has mated several times, because several queens coexist within the colony, or because of a combination of both factors. Differential exposure to environmental factors and different diets during development also produce a diversity of individuals.
4. *Flows*. A social insect colony is characterized by flows of nutrients and energy, of materials, and information.

Self-Organization in Social Insects

A Dynamic Approach

All of the ingredients and properties of CAS described in the preceding section emphasize the need for a dynamic, rather than static, approach to CAS. One such approach relies on self-organization (SO): theories of SO—originally developed in the context of physics and chemistry to describe the emergence of macroscopic patterns out of processes and interactions defined at the microscopic level (Haken 1977; Nicolis and Prigogine 1977)—have been extended to social insects to show that complex collective behavior may emerge from interactions among individuals that exhibit simple behavior (Deneubourg and Goss 1989; Bonabeau and others 1997). Models based on SO clearly assume dispersed interactions, the absence of global controller, and far-from-equilibrium dynamics; may either explicitly include or lead to a hierarchical organization; and produce adaptation and novelty: SO therefore provides a natural framework to describe and study CAS. In the context of social insects, an important consequence of the SO approach, which consists of viewing complex colony-level behavior as resulting from the interplay of (a) interactions among individual insects and (b) interactions between insects and their environment, has been to show that it is not always necessary to invoke individual complexity (the ability to take into account numerous parameters to modulate one's behavior) in order to explain complex colony-level phenomena or complex spatiotemporal patterns, the time and length scales of which go far beyond the characteristic time and length scales of individual insects.

Ingredients and Properties of Self-Organization

SO is a set of dynamic mechanisms whereby structures appear at the global level of a system from interactions among its lower-level components (Haken 1977; Nicolis and Prigogine 1977). The rules specifying the interactions among the system's constituent units are executed on the basis of purely local information, without reference to the global pattern, which is an emergent property of the system rather than a property imposed upon the system by an external ordering influence. The basic ingredients of SO, which are relevant to both social insects and ecosystems, are

1. Positive feedback, or amplification, which promotes the creation of structures. Examples of positive feedback include recruitment and reinforcement. SO relies on the amplification of fluctuations due to random walks, errors, random task-switching, and so forth. Fluctuations, such as preexisting or behavior-induced heterogeneities in the environment, can act as seeds from which structures nucleate and grow.
2. Negative feedback, which counterbalances positive feedback and helps stabilize the collective pattern: it may take the form of saturation, exhaustion, or competition.
3. In social insects, SO relies on multiple interactions, either directly among individuals, or among elements that can be manipulated by them, such as soil pellets, seeds, corpses, eggs, and larvae.

SO usually results in three important properties or signatures:

1. The emergence of spatiotemporal structures in an initially homogeneous medium.
2. The possible coexistence of several stable states, or multistability: structures emerge by amplification of random deviations, and any such deviation can be amplified, so that the system converges to one among several possible stable states, depending on initial conditions (path dependency). In ecosystems, the existence of alternative stable states is an important theoretical possibility that is starting to receive empirical support [for example, see Dublin and others 1990)].
3. The existence of (parameter driven) bifurcations, where the behavior of a self-organized system changes dramatically.

In their work on self-organization in ecosystems, Holling and colleagues (1996) show that these three properties can be found in models of ecosystems.

Examples

The double-bridge experiment (Deneubourg and Goss 1989) is one of the simplest examples of SO in social insects. In experiments with the ant *Linepithema humile*, a food source is separated from the nest by a bridge with two equally long branches A and B (Figure 1). Initially, both branches have the same probability of being selected: choices are made at random. But a few more ants randomly select, say, branch A, where they deposit pheromone, a chemical that attracts nestmates. The greater amount of pheromone on A stimulates more ants to select A and so forth. When the bridge's branches are not the same length, the shorter branch is selected more frequently by the same mechanism, that is, the amplification of initial fluctuations: the first ants returning to the nest take the shorter path twice, from the nest to the source and back, and therefore influence outgoing ants toward the short branch. This example illustrates the notions of positive feedback, amplification of fluctutations, and multiple interactions. If the experiment lasts for several hours, negative feedback also comes into play in the form of food-source exhaustion or satiation, preventing foraging from going on. Two of the three signatures of SO can also be observed in this example:

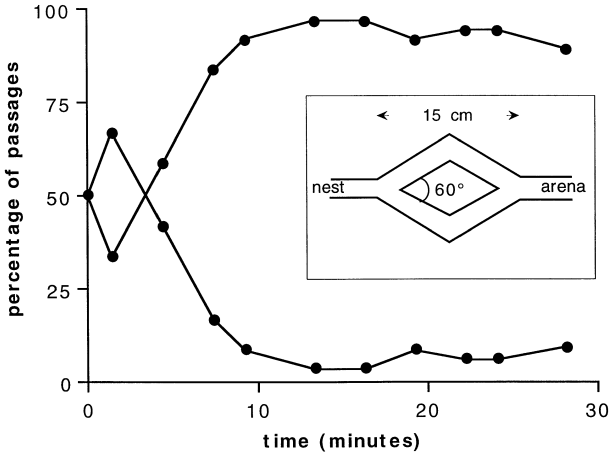

Figure 1. Double-bridge experiment (Deneubourg and Goss 1989). Percentage of all passages per unit time on each of the two branches as a function of time: one of the branches is eventually used most of the time. Note that the winning branch was not favored by the initial fluctuations, which indicates that these fluctuations were not strong enough to promote exploitation of the other branch. The *inset* is a schematic representation of the experimental setup.

1. *Emergence of structure*. In the case of equally long branches, the environment is initially homogeneous in that both branches are equally likely to be selected. The environment acquires structure, or loses its homogeneity, when one of the branches "wins."
2. *Multistability*. Depending on which branch is favored by initial fluctuations, either branch may eventually win. The system, therefore, has two stable states. This is true when both branches are the same length and also when they are not: in this latter case, initial fluctuations favor the short branch.

Another interesting example of SO is the construction of pillars by termites (Deneubourg 1977). The termite *Macrotermes* uses soil pellets impregnated with pheromone to build pillars (Figure 2). Two

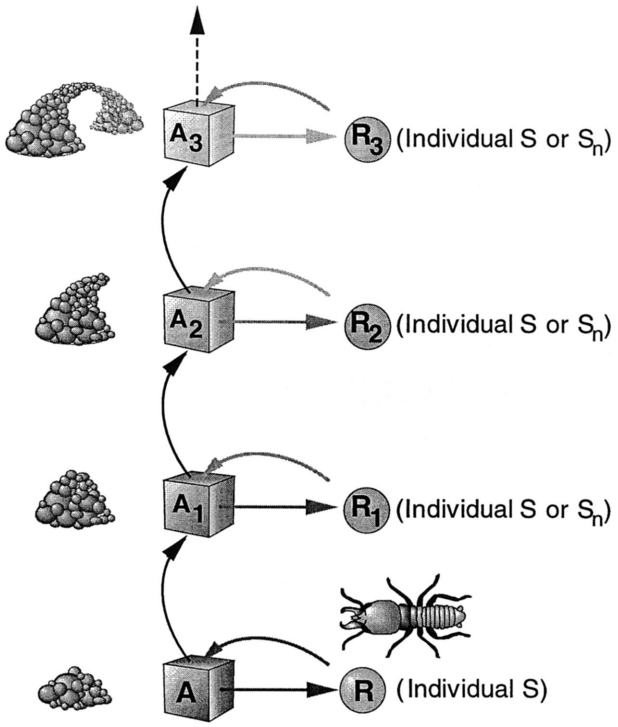

Figure 2. Schematic representation of the emergence of pillars in the termite *Macrotermes subhyalinus*. Successive building states leading to the emergence of a pillar and then of an arch joining two nearby pillars (A_1 to A_3), and the corresponding responses (R_1 to R_3) of the termite workers (Grassé 1959).

successive phases take place (Grassé 1959). First, the noncoordinated phase is characterized by a random deposition of pellets. This phase lasts until one of the deposits reaches a critical size. Then, the coordination phase starts if the group of builders is sufficiently large: pillars emerge. The existence of an initial deposit of soil pellets stimulates workers to accumulate more material through a positive-feedback mechanism, since the accumulation of material reinforces the attractiveness of deposits through the diffusing pheromone emitted by the pellets (Bruinsma unpublished PhD thesis 1979). This autocatalytic, "snowball effect" leads to the coordinated phase. If the spatial density of builders is too small, the pheromone disappears between two successive passages by the workers and the amplification mechanism cannot work. The system undergoes a bifurcation at this critical density: no pillar emerges below it, but pillars can emerge above it. This example illustrates several ingredients and signatures of SO:

1. *Positive feedback*. The accumulation of pheromone-impregnated material creates a snowball effect. Initial fluctuations are amplified: pillars tend to emerge where the first pellets have been dropped, because the first deposits attract more deposits.
2. *Negative feedback*. The decay of the pheromone limits the snowball effect.
3. *Multiple interactions*. Pillars emerge thanks to multiple indirect interactions among termites: one termite deposits a pellet, which stimulates another termite to deposit another pellet.
4. *Emergence of structure*. The initial spatial distribution of soil pellets is random. The activity of the termites transforms this random distribution into pillars.
5. *Bifurcation*. The spatial density of termites acts as a bifurcation parameter.

Direct and Indirect Interactions

Interactions among nestmates are either direct or indirect. Direct interactions include antennation, mandibular contact, or the exchange of fluid. Indirect interactions use the environment as a "medium of communication." In the two aforementioned examples, interactions are indirect. In the first example, ants lay pheromone in the environment, which influences other ants. In the second example, a pellet deposition by a termite influences other termites. This form of indirect communication through the environment is an extremely important aspect of collective coordination and has been coined *stigmergy* by Grassé (1959). Stigmergy is not only perfectly compatible with SO, it is also a major component of SO in many social insect examples because it mediates interactions among individuals. Stigmergy is likely to be relevant to the study of ecosystems, where many interactions among species within or across trophic levels are indirect. Stigmergy is also related to the concept of ecological engineering (Jones and others 1994; Lawton 1994; Pollock and others 1995; Naiman and Rogers 1997): "ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so, they modify, create and maintain habitats" (Jones and others 1994).

Usefulness and Limitations of Self-Organization

The recognition that complex colony-level behavior need not be rooted in complex individual behavior is one of the great advances that SO has enabled. Alternative approaches tend to assume that individuals have the ability to process huge amounts of information and make complex decisions, and that colony-level complexity is the phenotypic result of fine-tuned genotypic characteristics. For example, it

was not rare for students of social insects, until recently, to assume that the queen, one way or another, gives orders and centralizes information, or that rigid caste ratios (that is, the number of workers in each caste) have been optimized by evolution (Oster and Wilson 1978), with caste determination being largely genetic. It has now become clear that the queen, although she certainly plays a role in regulating some of the colony's activities, rarely gives direct orders and is unlikely to centralize information [for an exception, see Reeve and Gamboa (1987)], and that caste ratios in social insects are flexible rather than rigid (Calabi 1988). SO is an extremely plausible candidate to explain these features.

In addition to raising issues related to the group selection controversy, the CAS perspective, whereby it is assumed that colony-level behavior emerges through SO, is not always considered respectable because it often ignores external influences: the expression *self-organization* contains the error-inducing word *self*, which suggests that organization comes from *within*. Although approaches based on SO do emphasize that one must not overlook organizing factors that come from within, they do not deny the importance of external organizing forces: a combination of internal and external influences is most likely to constitute a relevant explanation in most examples of collective phenomena in social insects.

Beyond Self-Organization

SO is not the sole organizing mechanism of CAS. Even when it applies, SO alone usually does not provide sufficient explanation. In particular, environmental factors, acting as constraints or templates, most often play an essential role in determining what kind of colony-level organization is to be expected. For example, many ant species—including *Acantholepsis custodiens* (Brian 1983), *Formica polyctena*, and *Myrmica rubra* (Ceusters 1986)—use of temperature and humidity gradients in building their nests and in spatially distributing eggs, larvae, and pupae. Another obvious template is light, darkness and daylight certainly influence patterns of activity in most species of social insects and, for that matter, most animal species. More generally, the behavior of most insects is influenced by heterogeneities present in the environment. Insects tend to walk, build, store, or lay eggs along such heterogeneities. By heterogeneity, I mean any perceptible deviation from a uniform distribution or constant quantity, this includes irregular soil levels, obstacles, gradients, and predictably varying quantities such as temperature or light intensity. Sometimes, an individual can directly provide a template, as illustrated by the example of the construction of the royal chamber in termites (*Macrotermes subhyalinus*), the physogastric (filled with eggs) queen of *M. subhyalinus* emits a pheromone that diffuses and creates a pheromonal template in the form of a decreasing gradient around her (Figure 3). It has been shown experimentally that a concentration window or a threshold exists that controls the workers' building activities. A worker deposits a soil pellet if the concentration of pheromone lies within this window or exceeds the threshold (Bruinsma unpublished PhD thesis 1979; Bonabeau and others 1997, 1998). Otherwise, they do not deposit any pellet and destroy existing walls.

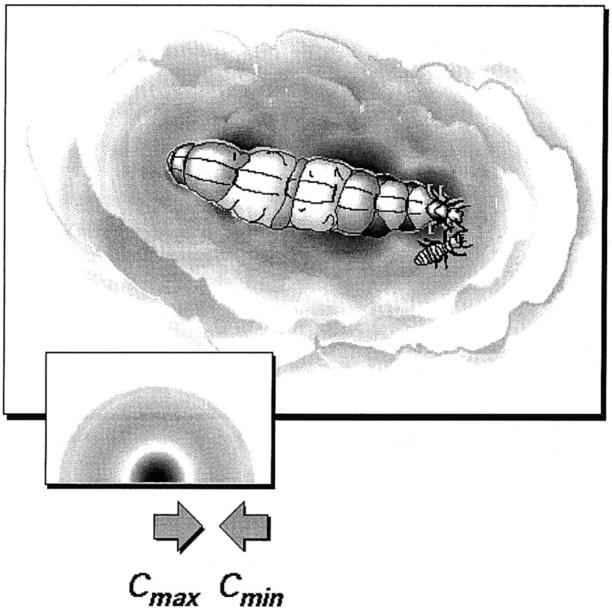

Figure 3. Sketch of pheromonal template, representing the physogastric queen and the king. Different pheromone concentrations are represented by different grey levels. [C_{max}, C_{min}] is the concentration window within which depositions are most likely to occur.

There may also exist more complex types of templates, those resulting from the colony's activities and that in turn influence the colony's future activities. Indeed, a single action by an insect results in a small modification of the environment that influences the actions of other insects. We have already met this mechanism, called stigmergy. A good example of a template that results from the stigmergic actions of individuals is the building of galleries along pheromone trails:

1. A trail network emerges because of the trail-laying–trail-following behavior of individual termites, which, as argued in the section of self-

organization among ants, is an example of stigmergy.
2. The trail pheromone diffuses away from the center of a reinforced portion of trail, thereby creating a chemical template, very similar in function to the queen's chemical template, along which walls are built.
3. Gallery size is adapted to traffic: the more termites, the higher is the pheromone concentration, and the further away from the trail center walls are built.

The important point is that this chemical template results from the termites' behavior and not merely from a preexisting heterogeneity. SO based on stigmergy and combined with templates is a powerful complexity-generating mechanism. Imagine a homogeneous medium in which structure emerges through SO and stigmergy—for example, pillars among termites. Once it has emerged, this structure is an heterogeneity that serves as a template that directs individual's actions. These actions, in turn, create new stimuli that trigger new building actions, either based on SO, templates, or both, and so forth. For example, nest building by termites is a morphogenetic process whereby complexity unfolds progressively (Bonabeau and others 1998): more and more complex structures appear as stimuli become more and more complex due to past construction.

DISCUSSION

I have presented the structure of social insects as an example of a CAS by arguing that large-scale patterns emerge from small-scale mechanisms through SO. I have presented a few select examples of SO in social insects in such a way that it could be useful to students of ecosystems who wish to take the CAS approach seriously. In particular, I have defined the basic ingredients and the key signatures of SO: knowing the important observable properties of SO (its signatures) enables identification of SO in natural systems; knowing the sources of SO (its ingredients) enables one to look for them. For example, knowing that positive feedback is the primary cause of SO should stimulate researchers to look for sources of positive feedback: reinforcement, recruitment, reproduction, imitation, and the like.

In addition to presenting ingredients and signatures of SO, I have introduced stigmergy (Grassé 1959), that is, indirect communication between individuals or constituent units through their environment. I have also introduced templates, which are preexisting or induced heterogeneities in the environment that are used by insects to organize some of their activities. Although it is often difficult to take the environment into account, it is extremely important to do so. The environment shapes individual behavior, which in turn determines colony-level behavior. If mechanisms that are internal to a system should not be overlooked, external forces must not be forgotten in the process of "internalizing" the causes of an observed phenomenon. SO, templates, and stigmergy set the stage for understanding the origin of the complexity of colony-level spatiotemporal patterns: although this understanding is far from complete, the complexity-generating mechanism sketched in the preceding section is promising, because it is general and also because it may provide a framework to study how past actions influence and constrain future actions so that complex patterns are produced robustly and consistently.

I conclude with an important question that has not been addressed in this report: what are the evolutionary implications of social insect colonies being self-organizing, complex adaptive systems? Since our understanding of collective behavior in social insects has significantly improved in the last decade with SO and the CAS approach, it is time to take the next step and place this emerging knowledge into an evolutionary framework. We, students of SO in social insects, have been a bit slow in taking this step, but it is now being taken (Bonabeau and others 1997). A parallel question can be asked about the evolution of ecosystems. Cross-fertilization of behavioral ecology and ecosystems science in respect to the evolution of CAS could be extremely useful. Two of Levin's (1998) concluding questions—how does evolution shape ecosystem properties, and does evolution increase resiliency or lead to criticality?—are indeed hot evolutionary questions when tranposed to social insects.

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