

# The Origin of Nest Complexity in Social Insects

*Learning from the models of nest construction*

## SOCIAL INSECTS: IMPRESSIVE ARCHITECTS AND BUILDERS

**A**mong the great variety of collective activities performed by social insect societies (all ants and termites, and some species of bees and wasps are social), building is certainly the most spectacular, owing to the difference that exists between the individual and collective levels [1-4]. This ability to build nests, some of which may be extremely complex, remains a fascinating issue for naturalists and scientists. The origin of nest complexity remains an unsolved mystery. Few works exist that deal with the analysis of the behavioral mechanisms involved in building and its regulation. Figure 1 shows some examples of nest architectures built by tropical wasps and African termites. Some species of wasps such as *Chartergus* (Figure 1a) or *Epipona* (Figure 1b) build nests made of several stacked combs of cells, and the external walls of the most peripheral cells are part of the external envelope of the nest. There is a central or peripheral communication opening that goes through the successive combs, allowing the wasps to move from one floor to another. Some paper nests built by *Polybia* wasps can be one meter high. In termites, some nests are literally cathedrals of clay that can reach six or seven meters high in *Macrotermes*, that is, 600 times the size of a worker.

A lot of species of termites build architectures comprised of a variety of delicate and highly regular structures. For instance, *Apicotermes* termites build subterranean oval nests about 20 cm high, in which one can find stacked horizontal chambers connected by helix-shaped vertical passages that are used as spiral staircases (Figure 1c). The outer surface of the nest is covered with a set of regularly spaced pores that open toward corridors circulating inside the internal wall of the nest. But social insect nests are more than the simple repetition of the same basic module; even if some basic elements are repeatedly present, they are organized in superstructures and networks. For instance, a beehive is not just an array of hexagonal cells: Cells are organized into combs, and each comb is organized into three distinct concentric regions, with a central area where the brood is located, surrounded by a ring of cells that are filled with pollen, and finally a large peripheral region of cells where honey is stored [5].

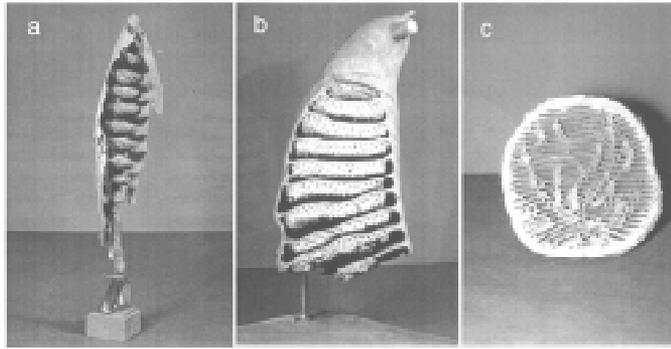
## THE ORIGIN OF NEST COMPLEXITY

What is the (ontogenetic) origin of nest complexity? Individual insects in social insect colonies have limited cognitive capabilities, and there is no evidence that the behavior of an individual in a social species is more sophisticated than that of an individual in a solitary species (where colony foundation, nest building, brood care, etc., are performed by single insects). Yet, only social insects seem to be capable of building the complex nests described above—although not all social insect colonies build such nests. Nests

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FIGURE 1(a-c)



(a) Nest of the wasp *Parachartergus*.  
(b) Nest of the wasp *Epipona tatau*.  
(c) Nest of the termite *Apicotermes arquieri*.

produced by solitary insects can most often be characterized by a simple repeated structure that contains only a few cells. The first hypotheses put forward to explain complex nest building in social insects were anthropomorphic: Individual insects were assumed to possess a representation of the global structure to be produced and to make decisions on the basis of that representation. Nest complexity would then result from the complexity of the insects' behavior. But there has been no experimental evidence for the use of a map or a blueprint by insects in building activities.

Insect societies are organized in a way that departs radically from the anthropomorphic model, where there is a direct causal relationship between nest complexity and behavioral complexity [6,7]. Recent work suggests that a social insect colony is a decentralized system comprised of cooperative, autonomous units that are distributed in the environment, exhibit simple probabilistic stimulus-response behavior, and have access to local information. Insects are equipped with a sensory-motor system (including chemoreceptors, mechanoreceptors, thermoreceptors, hygroreceptors, etc.) that enables them to respond to stimuli that are either emitted by their nestmates or originate from the environment.

Although such signals are not equiva-

lent to signs that could have symbolic value—these signals are simply attractive or repulsive, activating or inhibiting—they affect behavior in a way that depends on their intensity and on the context in which they are released: We begin to sense that nest complexity may result from the variety of stimuli that surround insects in a social context, as stimuli include not only environmental cues but also interactions among nestmates. The set of stimuli need not be stationary: For example, as a colony grows, starting from a single unhelped foundress, more and more stimuli are likely to appear because of the emergence of new individuals, thereby forming a richer and richer stimulatory environment for the insects. When applied to nest construction, this idea is very attractive: The stimuli that initially trigger building behavior may be quite simple and limited in number but, as construction proceeds, these stimuli become more complex and more numerous, thereby inducing new types of behavior. Construction can best be seen as a morphogenetic process during which past construction sets the stage for new building actions. The aim of this article is to illustrate this idea with a few examples. This principle can be coupled with the above-mentioned demographic effects: As the nest gets bigger, the greater the variety of signals and cues it is likely to encompass (the probability of finding

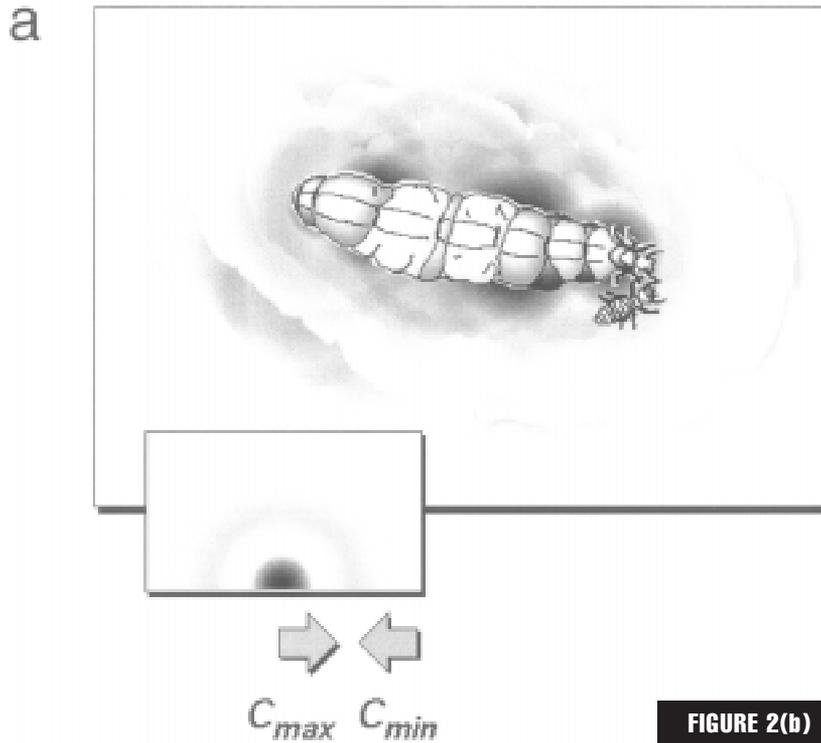
heterogeneities also increases when the colony expands its territory). This may explain why the most populous termite societies have the most complex nests [8].

### ENVIRONMENTAL CUES: TEMPLATES

A mechanism widely used by social insects to organize and coordinate their building activities relies on templates: The blueprint of the nest “already exists” in the environment under the form of physical or chemical heterogeneities. For example, many ant species (including *Acantholepsis custodiens* [9], *Formica polyctena*, *Myrmica rubra* [10], and *Messor ebenius* [11]) make use of temperature and humidity gradients to build their nests and spatially distribute eggs, larvae, and pupae. More generally, the behavior of most insects is influenced by heterogeneities in the environment: They tend to walk, build, store, or lay eggs along such heterogeneities. An heterogeneity is any perceptible deviation from a uniform distribution or constant quantity: This includes irregular soil levels, obstacles, gradients, predictably varying quantities such as temperature or light intensity, etc.

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 *Macrotermes subhyalinus* emits a pheromone that diffuses and creates a pheromonal template in the form of a decreasing gradient around her (Figure 2). It has been shown experimentally that a concentration window exists, or a threshold, that controls the workers' building activities: A worker deposits a soil pellet if the pheromone concentration lies within this window or exceeds the threshold [7,12,13]. Otherwise, they do not deposit any pellet or even destroy existing walls. If one places a freshly killed physogastric queen in various positions, walls are built at a more or less constant distance from the queen's body, following its contours, while a wax dummy of the queen does not stimulate construction. In this description, we have omitted for simplicity tactile stimuli and other pheromones, such as cement and trail pheromones, that fa-

FIGURE 2(a)



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

cilitate the recruitment, coordination, and orientation of individual workers, and that determine the detailed shape of the reconstructed chamber: The major organizing role is played by the queen's building pheromone, which creates a chemical template.

Observation of *Lasius niger* ants suggests another related type of influence from the environment. When humidity varies, a change in the shape of the craters built at the nest surface occurs: Crater shapes range from chimney-like after a rainfall to flattened discs when the excavated material is dry. The transporting and unloading behavior remains unchanged whatever the humidity. On the other hand, the cohesion of the building material strongly changes with humidity, which can by itself explain shape differences. *Lasius niger* ants have a hollow nest. Chambers inside the nest have

extremely different shapes depending on where the nest has been dug. In the upper parts of the nest that are built with soil particles from excavation, all chambers exhibit a sponge-like structure; in the subterranean part, one can clearly distinguish a network of galleries and chambers. The spongy structure of the upper parts can certainly be explained by the fact that soil is softer and less compact.

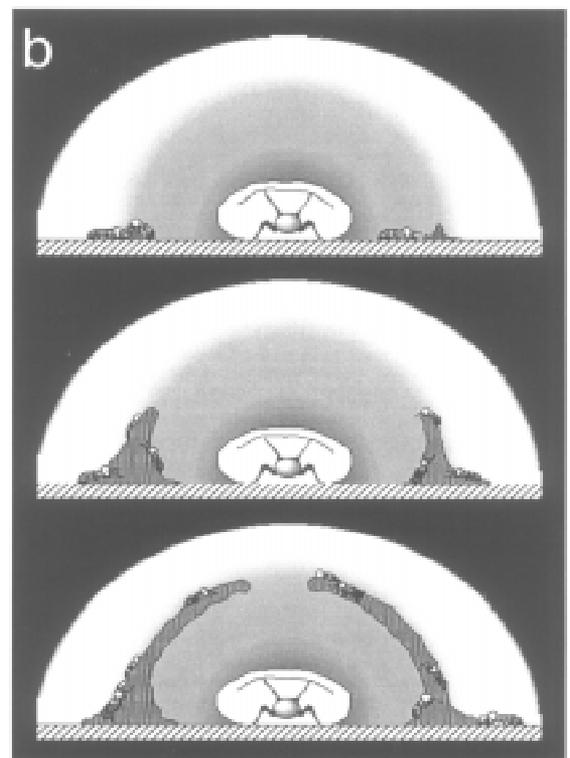
There may also exist more complex

types of templates: those heterogeneities that result 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: This form of indirect communication through the environment is an important aspect of collective coordination and has been coined "stigmergy" by Grassé [14].

### STIGMERGY

Grassé introduced stigmergy (from the Greek *stigma*: sting, and *ergon*: work) to explain task coordination and regulation in the context of nest reconstruction in termites of the genus *Bellicositermes* [8,14]. Grassé showed that the coordination and regulation of building ac-

FIGURE 2(b)



The template is three-dimensional. Workers may walk on top of the queen to make the ceiling of the chamber.

tivities do not depend on the workers themselves but is mainly achieved by the nest structure: A stimulating configuration triggers the response of a termite worker, transforming the configuration

into another configuration that may trigger in turn another (possibly different) action performed by the same termite or any other worker in the colony. In order to build their nests, termite workers use

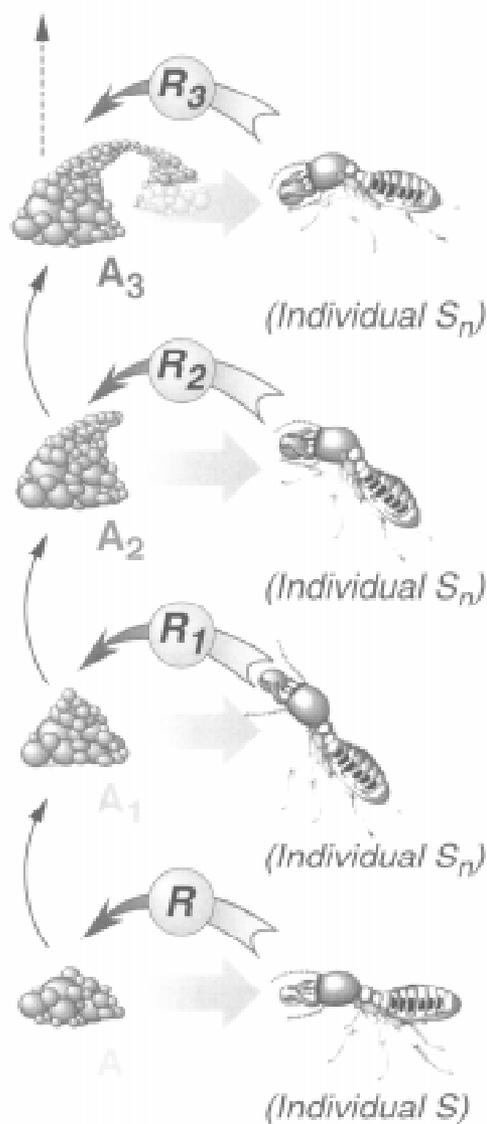
soil pellets or stercoral mortar. Nest reconstruction consists of first building strips and pillars with these pellets; arches are then thrown between the pillars and finally the inter-pillar space is filled to make walls. Figure 3 illustrates Grassé's [8,14] notion of stigmergy.

Stigmergy offers an elegant and stimulating framework to understand the coordination and regulation of building activities. But the main problem is to determine how stimuli are organized in space and time so as to lead to a robust and coherent construction: Colonies of a given species build qualitatively similar architectural patterns. Stigmergy is basically just a mechanism that mediates or implements worker-worker interactions: Therefore, it has to be supplemented with a mechanism that makes use of these interactions to coordinate and regulate collective building. Recent investigations suggest that at least two such mechanisms play a role in social insects: self-organization [6,7] and self-assembly [15,16].

### SELF-ORGANIZATION

**S**elf-organization (SO) is a set of dynamical mechanisms whereby structures emerge at the global level of a system out of interactions among its lower-level components [17,18]. 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 on the system by an external ordering influence. The basic ingredients of SO are [7]: (1) positive feedback (amplification), which promotes the creation of structures; examples of positive feedback include recruitment and reinforcement; (2) negative feedback, which counterbalances positive feedback and helps stabilize the collective pattern: it may take the form of saturation, exhaustion, or competition; (3) the amplification of fluctuations (random walks, errors, random task-switching, and so on): fluctuations, such as preexisting or behavior-induced heterogeneities in the environment, can act as seeds from which structures nucleate and grow; and (4)

**FIGURE 3**



Assume that the architecture reaches state **A**, which triggers response **R** from worker **S**. **A** is modified by the action of **S** (for example, **S** may drop a soil pellet) and transformed into a new stimulating configuration **A**<sub>1</sub> that may in turn trigger a new response **R**<sub>1</sub> from **S** or any other worker **S**<sub>n</sub> and so forth. The successive responses **R**<sub>1</sub>, **R**<sub>2</sub>, **R**<sub>n</sub> may be produced by any worker carrying a soil pellet. Each worker creates new stimuli in response to existing stimulating configurations. These new stimuli then act on the same termite or any other worker in the colony. Such a process, where the only relevant interactions taking place among the agents are indirect, through the environment that is modified by the other agents, is also called *sematectonic* communication.

multiple interactions, either directly among individuals or among elements that can be manipulated by them (in the context of social insects, soil pellets, seeds, corpses, eggs, larvae, etc.).

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 (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); and 3) the existence of (parameter-driven) bifurcations, where the behavior of a self-organized system changes dramatically.

**D**eneubourg [19] showed that SO, combined with stigmergy, can explain the construction of pillars in the termites studied by Grassé [8,14]. Workers use soil pellets impregnated with pheromone to build pillars. Two successive phases take place [14]. 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 or strips 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 attractivity of deposits through the diffusing pheromone emitted by the pellets [12]. This autocatalytic, snowball effect leads to the coordinated phase. If the density of builders is too small, the pheromone disappears between two successive passages by the workers, and the amplification mechanism cannot work, which leads to a noncoordinated phase. The system undergoes a bifurcation at this critical density: no pillar emerges below it, but pillars can emerge above it.

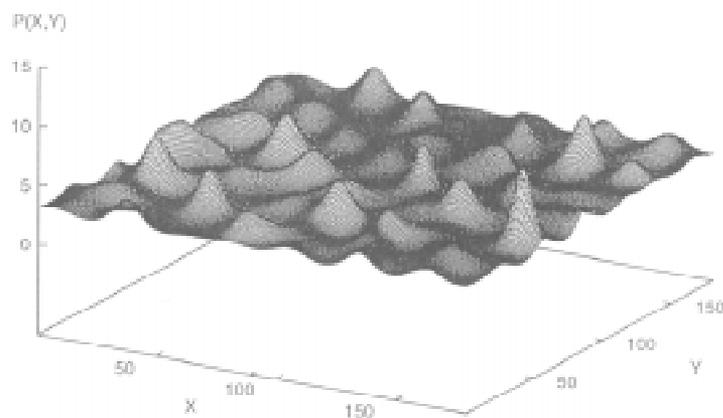
This example therefore illustrates positive feedback (the snowball effect), negative feedback (pheromone decay), the amplification of fluctuations (pillars could emerge anywhere), multiple inter-

actions (through the environment), the emergence of structure (that is, pillars) out of an initially homogeneous medium (that is, a random spatial distribution of soil pellets), multistability (again, pillars may emerge anywhere), and bifurcation. From the experimental observations, Deneubourg [19] designed a chemotaxis-based reaction-diffusion model that exhibits the desired properties for appropriate parameter values. Figure 4 shows the

two-dimensional spatial distribution of pillars obtained with his model. In this model, coordination emerges out of indirect (stigmergic) interactions among workers. Skarka et al. [20] provide another example of self-organization based on stigmergic interactions in comb construction in honey bees.

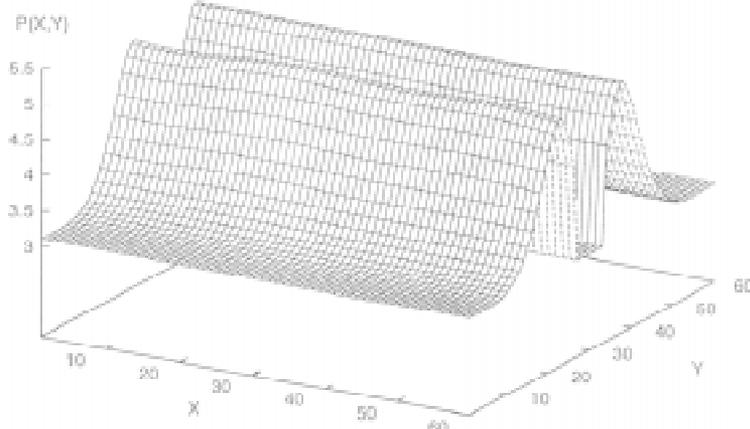
Bonabeau et al. [13] have extended this model to study the effects of various heterogeneities, such as convective

**FIGURE 4**



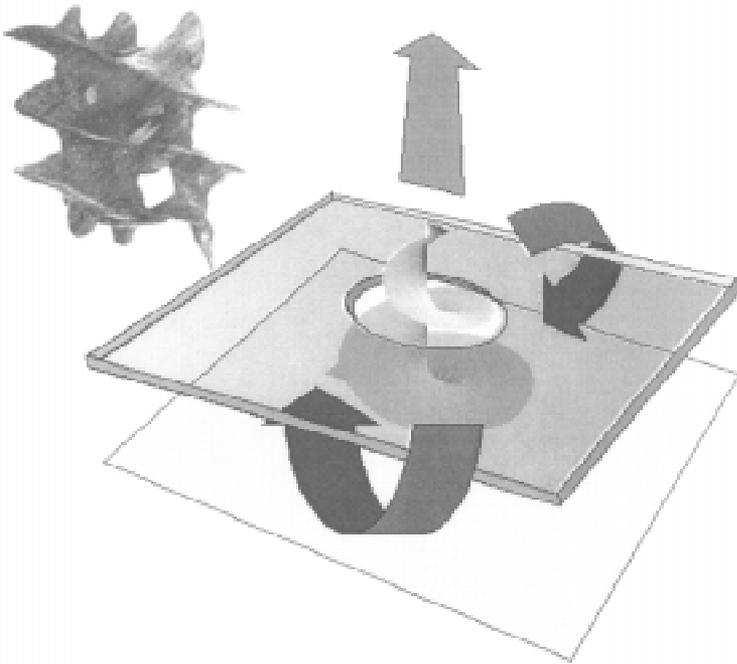
Spatial distribution of soil pellets obtained from Deneubourg's [19] model in two dimensions [13].

**FIGURE 5**



Pattern obtained with the same model as in Figure 4, now supplemented with a pheromone trail that attracts individuals and inhibits pellet deposits right on the trail [13].

FIGURE 6



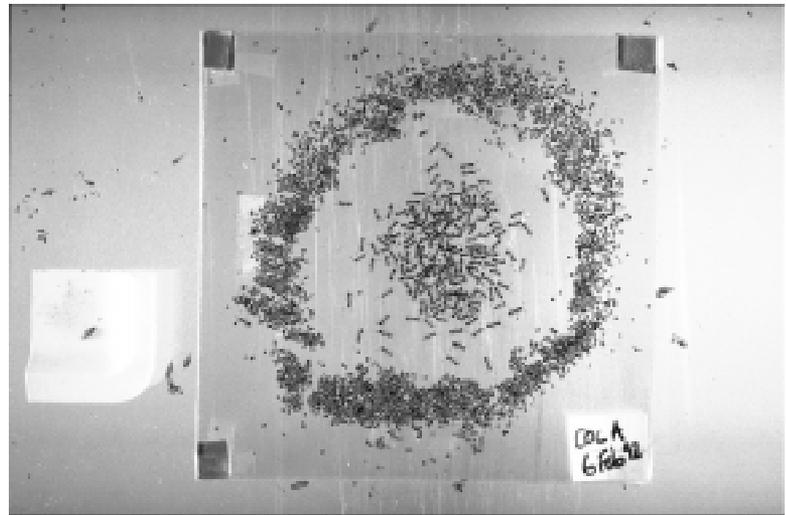
The possible role of convective air currents in the creation of complex three-dimensional chemical templates. Such processes could be involved in the construction of helicoidal structures that are used as access ramps to the various levels of the nest. Such structures have been found in the nest of the subterranean termite *Apicotermes arquieri* (top left).

individual termites. Note in passing that this mechanism allows gallery size to be adjusted to traffic: The chemical template formed by the trail grows with termite density. This provides us with a clear picture of a powerful complexity-generating mechanism: Imagine an homogeneous medium in which structure emerges through SO and stigmergy (for example, pillars in termites); once it has emerged, this structure is a heterogeneity that serves as a template that canalizes individuals' actions; these actions create in turn new stimuli that trigger new building actions, either based on SO or templates or both; and so forth. Nest building is a morphogenetic process whereby complexity unfolds progressively [13]: More and more complex structures appear as stimuli become more and more complex due to past construction.

To illustrate how a highly complex succession of patterns could emerge, let us describe another possible application of templates and stigmergy, albeit more speculative, to the construction of helicoidal access ramps in nests of termites *Apicotermes arquieri*

air flows, flows of individuals, trail networks. They show that, although individual behavior may not be modified by such heterogeneities, new structures appear because the organization of the stimuli is different, influenced by the heterogeneities. For example, in the presence of a pheromone trail, the same mechanism that leads to the emergence of pillars when there is no pheromone now produces galleries along the trail (Figure 5): The trail pheromone diffuses away from the center of the trail, thereby creating a chemical template, very similar to the queen's chemical template, along which walls are built in a self-reinforcing way because of the cement pheromone. What is remarkable here is that the template generated by the trail is no longer a preexisting heterogeneity imposed on the colony by the environment or by the queen: The template results from the colony's activities. Indeed, a trail network emerges because of the trail laying-trail following behavior of

FIGURE 7



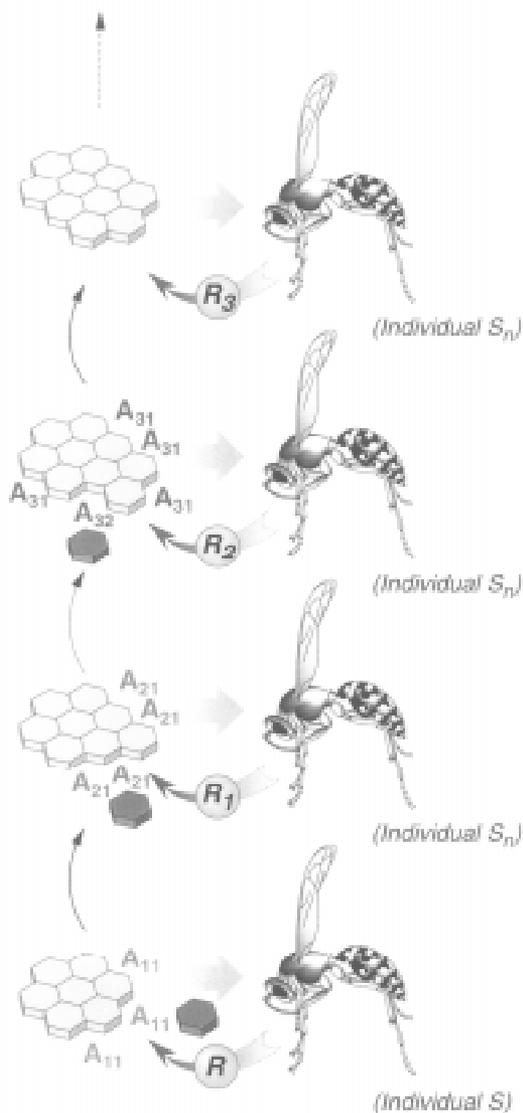
*Leptothorax tuberointerruptus* nest in the laboratory. The ants have been given a 0.8 mm deep cavity between 80 mm x 80 mm glass plates. They have built a dense wall from sieved sand. The worker ants, each approximately 2.5 mm in length, are densely clustered around the central queen and the brood. © Nigel R. Franks, with permission.

(Figure 1c). It is well known that termites are highly sensitive to air currents and that stable complex convective air currents are taking place within termite nests. Such currents can carry with them molecules of pheromone (soil pellets are impregnated with pheromone), thereby creating a complex chemical template that workers materialize (Figure 6). Of course, the interplay between such structures, built along complex chemical fields, and air currents that produce the fields (and are modified by new building actions) is quite complex and difficult to study, either mathematically or experimentally. But this speculation deserves to be kept in mind, and studying the initiation of the process is not out of reach of experiments.

**A**nother example where the colony's activities may lead to the formation of a template used to construct a nest is wall building in the ant *Leptothorax*: The brood is used as a template to build walls at a given distance from the brood [21,22] (Figure 7). This example looks similar to the reconstruction of the royal chamber in termites. Here, however, the brood has been compactly aggregated by the workers prior to the construction of the walls: It is interesting to note that the brood-clustering process is itself self-organized [23].

Bonabeau et al. [13] also show that, as previously mentioned, colony growth can act as a source of nest complexity. Nest growth is generally correlated to the growth of the population that lives inside the nest. When the growth of the colony occurs through successive bursts, the corresponding nest structure will consist of a succession of similar modules stacked together as it is the case in *Cubitermes* or *Noditermes* termites [8]. However, nest growth is not necessarily a simple function of demography. For example, a centrifugal flow of individuals may be observed as population increases, leading to heterogeneities in population distribution: Such heterogeneities may lead to new types of structures. In some cases, the nest grows by bursts despite the fact that population size increases steadily. Deneubourg and Franks [24] have shown with a simple model how this can hap-

**FIGURE 8**



The equivalent of Figure 3 for wasps: Local configurations of cells around the nest are modified each time a new cell is added by a wasp. Only a small number of these configurations trigger the addition of a new cell.

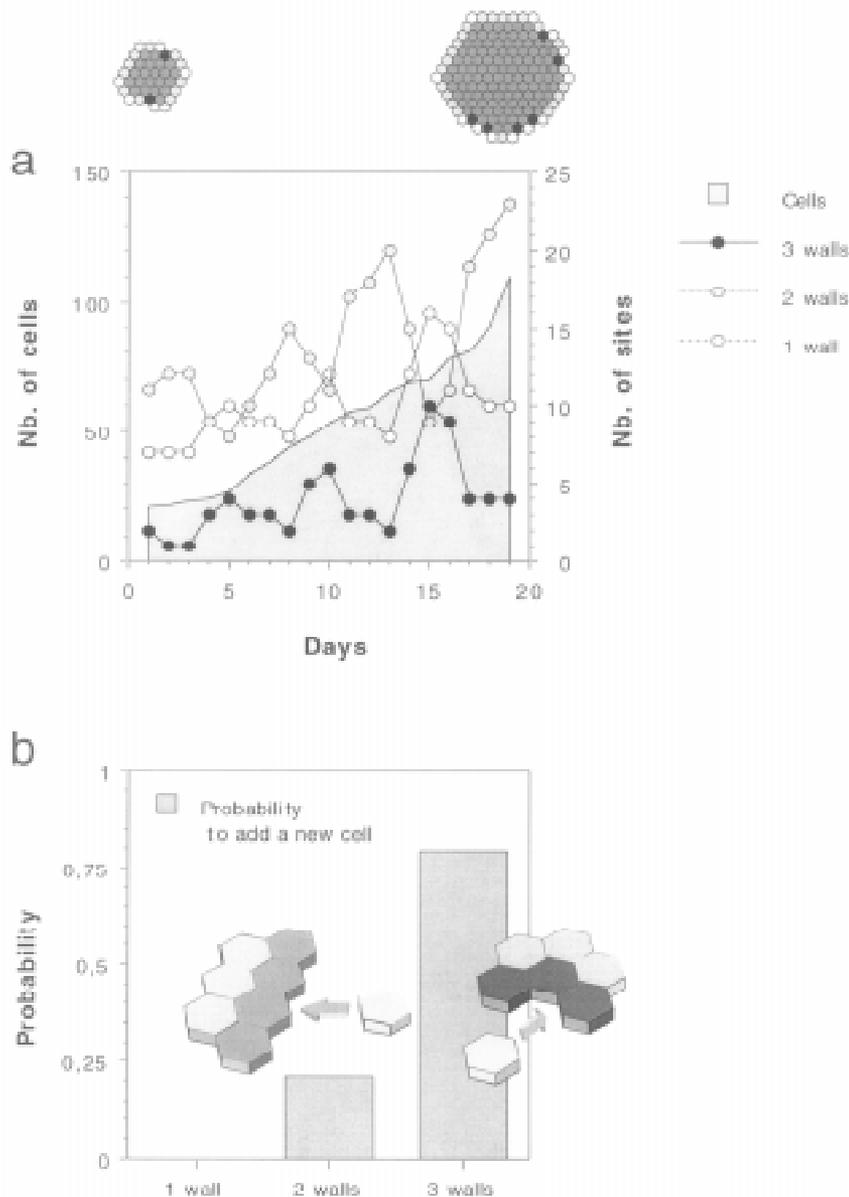
pen: When stimulated to build because population density has increased beyond a given threshold, insects may dig more than just what is needed to accommodate newly emerged individuals and bring the population density back below threshold. This is because workers mutually stimulate each other into digging, which results in a snowball digging effect. Many workers participate in this process, so that population density quickly goes well be-

low threshold, where the workers lose their motivation to dig, until population density exceeds their response threshold again.

#### SELF-ASSEMBLY

**S**elf-assembly, which we may also call qualitative stigmergy in the context of this article, differs from SO in that individuals interact through, and respond to, *qualitative* stimuli: When

FIGURE 9(a,b)



(a) Development of a wasp nest structure (*Polistes dominulus*) and dynamics of the local building configurations.  
 (b) Differential probability to add a new cell to a corner area where three adjacent walls are present and on the side of an existing row where two adjacent walls are present.

termites build pillars, they respond to *quantitative* stimuli, namely, pheromone fields and gradients. Self-assembly is based on a discrete set of stimulus types: For example, an insect responds to a type-1 stimulus with action A and responds to a type-2 stimulus with action B. In other

words, qualitatively different stimuli result in qualitatively different responses. It is easy to see how such a mechanism is still compatible with stigmergic interactions: For example, a type-1 stimulus triggers action A by individual  $I_1$ ; action A transforms the type-1 stimulus into a

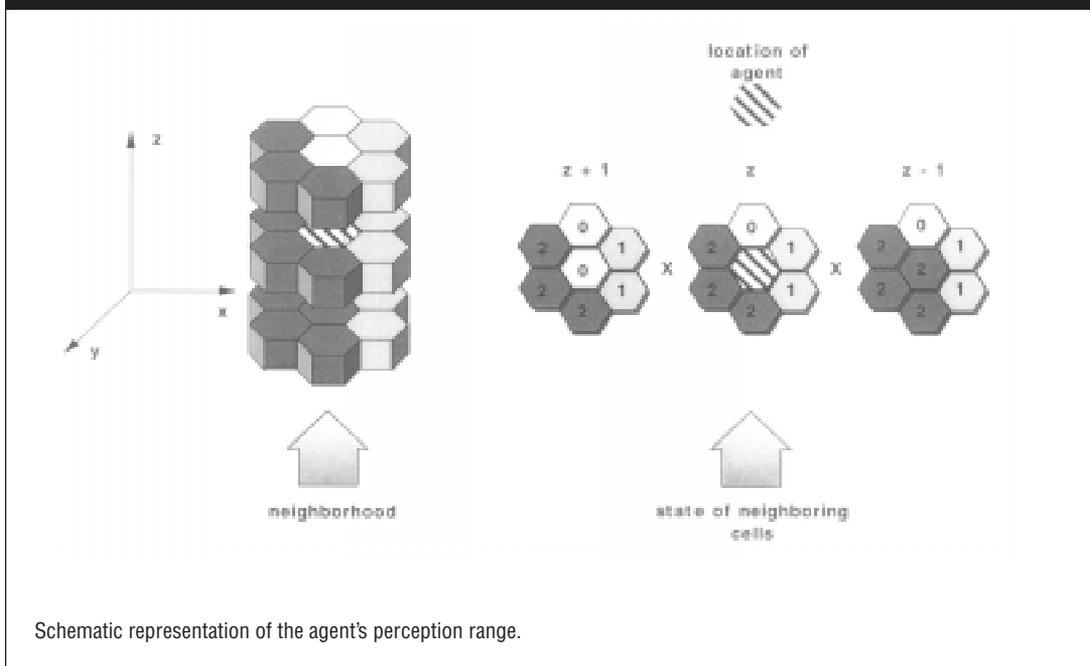
type-2 stimulus that triggers action B by individual  $I_2$ .

But why call this process self-assembly? Imagine that each individual is carrying a building element, such as a soil pellet or a load of wood pulp, of a certain type and deposits this element only when specific conditions are met, for example, when that individual is surrounded by three walls: The building element will be added to the individual's current location under these conditions. Therefore, from the viewpoint of the building element, a form of self-assembly, mediated by the individual, is taking place: Building elements self-assemble whenever appropriate. It is more difficult, however, to see how coordination and regulation can be achieved in self-assembly. Building in social wasps seems to provide an example of qualitative stigmergy (Figure 8). Theraulaz and Bonabeau [15,16,25] have introduced a model, inspired by the building behavior of wasps (see also [26]), that illuminates how coordination may emerge and clarifies the meaning of self-assembly.

**S**ocial wasps have the ability to build nests that range from very simple to highly organized. Nests are made of plant fibers that are chewed and cemented together with oral secretion. The resulting carton is then shaped by the wasps to build the various parts of the nest (pedicel, walls of cells, or external envelope). Wenzel [3] has classified wasp nest architectures and found more than 60 different types, with many intermediates between extreme forms. A mature nest can have from a few cells up to a million cells packed in stacked combs, the latter being generally built by highly social species. Modularity is another widespread feature of nest architectures: a basic structure is repeated.

Previous studies showed that individual building algorithms consist of a

FIGURE 10



a brick) by an agent depends on the local configuration of bricks in the cells surrounding the cell occupied by the agent (Figure 10). Two types of bricks can be deposited. No brick can be removed once it has been deposited. All simulations start with a single initial brick. A micro-rule is defined as the association of a stimulating configuration with a brick to be deposited, and we call algorithm any collection of compatible micro-rules.

Two micro-rules are

series of if-then decision loops [27,28]. The first act usually consists, with only a few exceptions, in attaching the future nest to a substrate with a stalk-like pedicel of wood pulp [3]. Then, wasps initiate the nest by building two cells on either side of a flat extension of the pedicel. Subsequent cells are added to the outer circumference of the combs between two previously constructed cells. As more cells are added to the evolving structure, they eventually form closely packed parallel rows of cells and the nest generally has radial or bilateral symmetry around these initial cells. A wasp tends to finish a row of cells before initiating a new row, and rows are initiated by the construction of a centrally located cell first.

**T**he number of potential sites where a new cell can be added increases significantly as construction proceeds: Several building actions can in principle be made in parallel—and this is certainly an important step in the emergence of complex architectures in the course of evolution. Parallelism, however, could deorganize the building process by introducing the possibility of conflicting actions being performed simultaneously. But the architecture seems to provide enough constraints to

canalize the building activity. It can be seen, with a careful study of the dynamics of local configurations of cells during nest development in the primitively eusocial wasp *Polistes dominulus*, that there are not equal numbers of sites with one, two, or three adjacent walls. The great majority of them are composed of sites with two adjacent walls (Figure 9a). Cells are not added randomly to the existing structure: Wasps have a greater probability to add new cells to a corner area where three adjacent walls are present than to initiate a new row by adding a cell on the side of an existing row (Figure 9b). Therefore, obviously, wasps are influenced by previous construction, and building decisions seem to be made locally on the basis of perceived configurations in a way that possibly constrains the building dynamics.

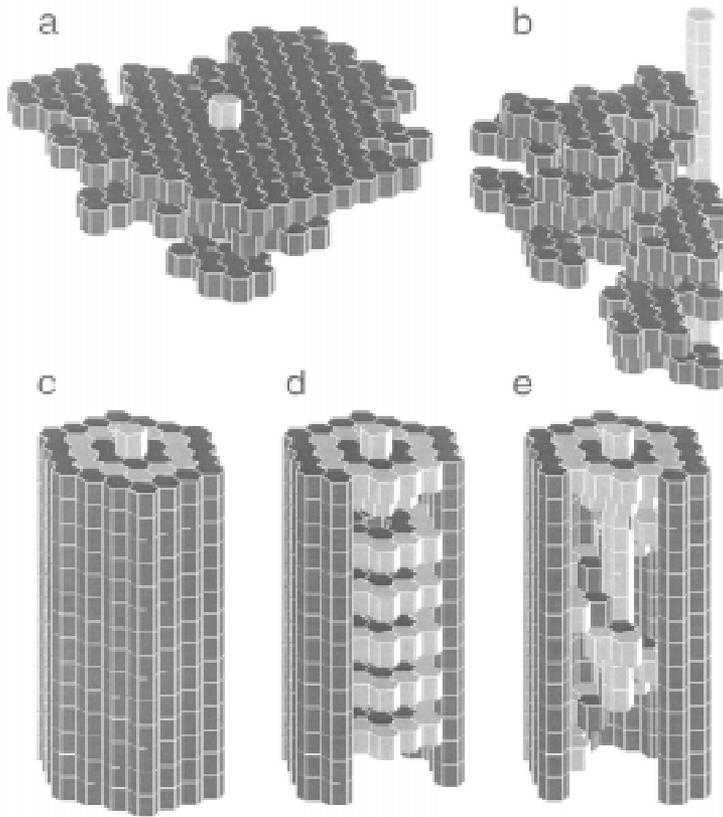
In order to explore the potential of self-assembly as a model of nest construction, Theraulaz and Bonabeau [15,16,25] introduced a class of algorithms that could hardly be made simpler: asynchronous automata that move in a three-dimensional discrete space and take actions on a pure stimulus-response basis, relying on information that is local in space and time. The deposit of an elementary building block (hereafter called

not compatible if they correspond to the same stimulating configuration but lead to the deposition of different bricks. An algorithm can be characterized by its micro-rule table, basically a lookup table, comprised of all its micro-rules, that is, all stimulating configurations and associated actions.

**A** single agent in this model is able to complete an architecture. In that respect, building is a matter of purely individual behavior. But the individual building behavior, determined by the local configurations that trigger building actions, has to be organized in such a way that a group of agents can produce the same architecture as well. Some natural wasp species face the same problem since nest construction is generally first achieved by one female, the founder, and is then taken over by a group of newly born workers. The group of agents has to be able to build the architecture without the combined actions of the different agents interfering and possibly destroying the whole activity of the swarm.

It was possible to produce complex shapes, some of them strikingly similar to those observed in nature, with algorithms belonging to this simple family [25] (Figure 11). Theraulaz and Bonabeau [15,16]

**FIGURE 11**



Simulations of collective building on a three-dimensional hexagonal lattice. Simulations were made on a  $20 \times 20 \times 20$  lattice with 10 wasps. Some architectures are reminiscent of natural wasp nests and exhibit a similar design.

(a) Nest-like architecture (*Vespa*) obtained after 20,000 steps.

(b) Nest-like architecture (*Parachartergus*) obtained after 20,000 steps.

(c, d) Nest-like architecture (*Chartergus*) obtained after 100,000 steps. A portion of the front envelope has been cut away in 12d.

(e) Lattice architecture including an external envelope and a long-range internal helix. A portion of the front envelope has been cut away.

found *a posteriori* that structured shapes can be built only with special algorithms, coordinated algorithms, characterized by emergent coordination: Stimulating configurations corresponding to different building stages must not overlap, so as to avoid the deorganization of the building activity. This feature creates implicit handshakes and interlocks at every stage, that is, constraints upon which structures can develop consistently and robustly. This coordination is essential, since parallelism, which has a clear adaptive advantage by allowing a real colony to build at several locations at the same time, introduces the possibility of conflicts. This approach

(which is described at length in [15, 16, 25]) therefore shows how the nest itself can provide the constraints that canalize a stigmergic building behavior into producing specific shapes.

## DISCUSSION

**W**here do we stand? We have presented a few models of nest construction in social insects based on four, usually intertwined, mechanisms: templates, stigmergy, self-organization, and self-assembly. These models are still to a large extent speculative: Experimental evidence is scarce. However, three important lessons can be

drawn from studying these models.

1. *It may not be necessary to invoke individual complexity to explain nest complexity.* Apparently different behaviors from the same individual may result from the same type of response in different environmental or social conditions: We have seen, for example, that the level of humidity influences what structures are observed in nests of the ant *Lasius niger*, not because individuals change their behavior in response to humidity (although they may be sensitive to this parameter), but because the physical properties of the soil particles are different. Again, given the current body of empirical data on nest building, one cannot completely rule out individual complexity. However, most ethologists would tend to assume, in the example of nest building in *Lasius niger*, that workers build differently when humidity is high. Our bias is just the opposite: There may be a simpler explanation.

2. *The complexity of a nest is likely to result from the unfolding of a morphogenetic process during which past construction provides both constraints and new stimuli.* Templates, stigmergy, self-organization, and self-assembly are the building blocks of a powerful construction game. The parallel with morphogenesis in embryology is striking [29]: Templates are the equivalent of gradients (for example, the expression of maternal RNA in an embryo leads to a gradient of proteins along the antero-posterior axis, which leads to the differential expression of genes in otherwise identical cells [30]), self-organization has been invoked to explain the alternance of stripes of gene expression [31], and self-assembly has been invoked to explain the formation of viruses (a related morphogenetic mechanism is differential adhesion [30]). Issues of interest in both nest construction and embryogenesis include the study of robustness, the identification of regulatory mechanisms, the understanding of responses to perturbations, of differentiation (behavioral or material for insects, cellular for embryos), and,

of course, of evolutionary implications. This analogy points to the question of whether there exist a few morphogenetic mechanisms implemented in various media across virtually all scales and taxa in biology, or is the analogy purely metaphorical?

3. *It may not be possible to oppose, behav-*

*iorally, solitary and social species, at least in the context of construction.* It is conceivable, and actually likely if one believes the models, that solitary and social insects have a similar building behavior, but the variety of stimuli encountered in a social context, combined with a numerical effect that accelerates construction and therefore

provides individuals with constantly new building stimuli, may be sufficient to explain the difference between the relative simplicity of nests built by solitary insects and the potentially enormous complexity of nests built by social species. In that respect, solitary insects would be pre-adapted to social life.

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