A Brief History of Stigmergy

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Abstract Stigmergy is a class of mechanisms that mediate animal-animal interactions. Its introduction in 1959 by Pierre-Paul Grassé made it possible to explain what had been until then considered paradoxical observations: In an insect society individuals work as if they were alone while their collective activities appear to be coordinated. In this article we describe the history of stigmergy in the context of social insects and discuss the general properties of two distinct stigmergic mechanisms: quantitative stigmergy and qualitative stigmergy.

Keywords
stigmergy, coordination, social insects, self-organization, self-assembling

1 Introduction

When the concept of stigmergy was first introduced in 1959 by French zoologist Pierre-Paul Grassé, an important step toward understanding the mechanisms underlying the emergence, regulation, and control of collective activities in social insects was made [26]. Until then two antagonistic theories had been attempting to deal with how insects coordinate their activities in a social insect colony. Some scientists considered that entirely new properties appeared at the level of the society. This level of biological organization, they believed, possesses its own laws and requires its own causal system to be understood: From their perspective, it is the "whole" that explains the behavior of the parts. At the other extreme, others considered that each individual in an insect society behaves as if it were alone: Any collective behavior or division of labor that would appear at the colony level was thought to exist only in the eye of the beholder. Stigmergy helped researchers understand the connection between the level of the individual and the level of colony, showing that an alternative theory could explain the "paradox" of coordination in social insects: Although the behavior of the colony as a whole looks wonderfully organized and coordinated, it seems that every insect is pursuing its own agenda without paying much attention to its nestmates. After a brief historical survey of pre-stigmergic theories (Section 2), some of which are still alive today in the biology community (see, e.g., [35]), we will show how the concept of stigmergy provided an elegant explanation to the coordination paradox. We will finally describe some recent advances in the application of stigmergy to understanding social insects (Section 3); in particular, we will introduce a subdivision of stigmergy into quantitative stigmergy and qualitative stigmergy. Although our focus will be social insects, the scope of stigmergy is clearly immense.

2 From the Superorganism to Stigmergy

2.1 Insect Societies as Superorganisms

The collective behavior of social insects has been a puzzling problem for philosophers and scientists for a long time. How is it possible for such simple creatures to coordinate

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their actions, create complex patterns, and make up such complex "republics" sometimes held up as examples for human society? For instance, how are myriads of bees able to adjust their actions so precisely when they build their hive? How is it possible to understand such a coordination? Everything happens for the observer as if there were a coordinating agent "virtually" present at the center of the colony. The first authors who tried to understand this astonishing phenomenon used an organicist metaphor. As was put forward by Herbert Spencer during the second part of the 19th century, any society is an organism [42]. Between what he called the *social organism* and any other living system, Spencer pointed out a whole set of common characteristics: growth, progressive and joint differentiation of structures and functions, mutual shaping of the parts they are made of, division of labor, and finally similar properties between the social organism and each of its constituent units, with the exception that the former has a greater lifetime. In 1877, French scientist and philosopher Alfred Espinas was the first author to apply this metaphor to describe the behavior of animal societies [20]. He was convinced that whatever the level of biological organization considered, living units are specifically charaterized by their tendency to join together into ever bigger units; in this way, the formation of societies from individuals appeared just as an extension of the natural trend of cells to assemble into multicellular organisms.

During the 20th century, the organicist metaphor continued to expand in science. In 1911, American entomologist William Morton Wheeler wrote a famous paper entitled *The ant colony as an organism*, in which he introduced what can be considered as the first *systemic* approach to the study of social phenomena in insects [46]:

> An organism is a complex, definitely coordinated and therefore individualized system of activities, which are primarily directed to obtaining and assimilating substances from an environment, to producing other systems, known as offspring, and to protecting the system itself and usually also its offspring from dangers emanating from the environment. The three fundamental activities enumerated in this definition, namely nutrition, reproduction and protection, seem to have their inception in what we know, from exclusively subjective experience, as feelings of hunger, affection and fear respectively.

Wheeler justified his assertions by considering the fact that both a society and a single organism share common features. Both behave as a single unit. Both show some idiosyncrasies that are peculiar to the species, in behavior, size, and structure, and other idiosyncrasies that distinguish one colony from another belonging to the same species. Both undergo growth and reproduction cycles that are clearly adaptive. Finally, both are differentiated in the same way: Queens and males would appear to be the equivalent of a germ plasma while the workers should be equivalent to the cellular soma. If these features may easily be dismissed as mere analogies, similar to those used by Spencer, they clearly had in Wheeler's mind a deeper meaning. Indeed, Wheeler suggested that there might exist within an insect colony, some *functioning constraints* that allow the whole society to behave as if it were a single and unique organism. The organization of a society must therefore be controlled by laws similar to those that govern any living organism: This would be sufficient to explain how coordination is achieved. Unfortunately, the scientific tools and concepts available at the time were useless in identifying such laws and Wheeler ended its study with the following observation [47]:

> [W]e can only regard the organismal character of a colony as a whole, as an expression of the fact that it is not equivalent to the sum of its individuals but that it represents a different and at present inexplicable emergent level.

Wheeler did not use the term *superorganism* until 1928, when his ideas on that matter had somewhat changed. As was underlined by E. O. Wilson [49], the notion of superorganism was initially used to describe homeostatic processes: "We have seen that the insect colony or society may be regarded as a super-organism and hence as a living whole bent on preserving its moving equilibrium and integrity" [48 p. 29].

In the following years, the notion of a superorganism was revived by another American entomologist, Alfred E. Emerson, in a series of general papers on social insects in which he also emphasized the homeostatic properties resulting from social dynamics [14–19]. But for Emerson the supraorganism, as he preferred to call it from 1950 on, remained a strict analogy-based concept with the aid of which he hoped to detect the similarities that could have appeared in the course of evolution between an insect society and a living organism. In particular, if an insect colony represents a distinct unit of selection, strong parallels can be drawn between the adaptive structures that can be found within a colony and those that characterize a single organism. Such adaptive structures must have evolved in both cases to improve the homeostasis of the whole machinery. In this way, the progressive improvements of division of labor, communication and trophallactic exchanges between insects, the partition into a soma (the workers) and a germen (the reproductive queens and males) are intended to increase the regulatory ability of a colony to reach a near-optimal adaptation. Emerson's attempt put a temporary end to the use of the organicist theory. This attractive analogy did not provide any insight because it did not have any explanatory value. It thus remained a mere metaphor with which it was easy to find similar global properties in a society and a single organism, yet without providing any information on the underlying mechanisms that induce these similarities. Higher-level laws of organization can only be discovered through analytical methods that require both a deep understanding of individual insect behavior and a careful examination of the way in which interactions among and exchanges between individuals regulate the collective behavior observed at the level of the colony.

2.2 Insect Societies as Collections of Independent Individuals

Since the 1930s the study of individual behavior within a society, which is often associated with an analytical approach, has spread rapidly, sometimes at the expense of an oversimplification of the real nature of social phenomena. The most significant scientist who used this approach was French biologist Etienne Rabaud, who was suspicious of any holistic explanation. His fundamental postulate was that the only cause of behavior lies within an individual. In his mind any other theory was mere metaphysical speculation [37]. His entire work on insect societies was an attempt to demonstrate that each individual insect in a society behaves as if it were alone, as it appears in this text describing building behavior in paper wasps [38]:

> In this way, each worker is indistinctly in charge of any part of the nest. Is this cooperation? In any case, if cooperation occurs it is only by chance and as a result of unexpected incidents. Are these building wasps following a general plan? When the founding female starts building its nest she decides to place it in a certain way. It seems that workers that come after on the nest continue the foundress's work in a well defined direction. In fact, they build cells without any regularity, but they build it in the same way the foundress did, in particular they enlarge the envelope as the number of cells in the comb increases. All this does not involve any prerequisite plan at all. This simply means that both the founding female and the workers are responding in the same way and with the same reflexes to the same stimuli. . . . In fact, whether they are isolated or in group, all individuals behave in the same way; whether they carry on their own work or that of the others, the entire environmental conditions remain exactly

> the same; in any case, everything happens as if they were doing their own work, without paying attention to their neighbors' work that exerts in this respect no noticeable influence on them. Apparently, a contradiction is emerging from these facts; in appearance only, because nothing in the work resulting from the combined efforts by several individuals is different from the work that is done by a solitary founding female. Only the speed at which cells are built increases because the size of the group is large enough. Thus all these individuals are working in the same way and each one is working as if it were alone; the "collective" work is only the juxtaposition of individual works. Neither the enlargement of the nest, nor the feeding of the larvae require that a whole plan has to be executed in such a way that a task performed by an individual induces that of his neighbor and conversely: [T]he common work is no more than a side effect of interattraction that gather[s] individuals together. (pp. 150–151)

Rabaud considered that division of labor requires as a precondition that a common sign code be used by the members of a society, which, according to him, was quite out of the question in the case of insects. Such a dogmatic assertion was unacceptable at the time it was put forward and is even less acceptable today, when numerous examples of social coordination are clearly established. This theoretical option was motivated by a relentless fight against mentalism and anthropomorphism.

Nevertheless, the anti-organicist controversy in which Rabaud was involved, despite its excess, led to the introduction of two concepts that turned out to be of utmost importance for understanding collective phenomena.

The first concept is that of interaction. Rabaud claimed that individual behavior was the essential drive of any collective action or process. In social animals that constantly live next to each other, one individual's action may influence another individual, thereby modifying its behavior. The term interaction refers to this kind of reciprocal action. Any social mechanism might be reduced to a set of elementary interactions. This simple idea opened the road for a research program that broke with the organicist theory by establishing a bridge between the individual and collective levels instead of considering them separately and independently.

The second concept introduced by Rabaud is interattraction, which he defined as a basic social phenomenon: Interattraction refers to the fact that any animal that belongs to a social species is attracted in a specific way by any other animal that belongs to the same species [38]. It is a specific interaction that can be triggered by the stimuli that individuals bear. One consequence of these interactions is a nonrandom distribution of individuals in the environment. This idea and its main consequences were later developed by Grassé [27]:

> Social groups are above all characterized by the fact that any individual taken separately produces a specific stimulus upon its fellows, while the group (that can be reduced to a single fellow) produces in turn a specific stimulus that will influence the behavior of that animal. (p. 8)

Rabaud clearly overlooked such consequences, particularly the fact that the emergence of a collective and coordinated behavior inside a society can be explained by a set of specific interactions among individuals.

2.3 The Organizing Role of Interactions and Stigmergy

At the same time Rabaud was conducting his research, a growing number of scientists, sometimes with more of a naturalist than a theoretical background, discovered that



Figure 1. Pierre-Paul Grassé (1895–1985) was the coordinator of a masterpiece treatise of zoology and a synthetic work on termites. He was also at the origin of the publication of the Bulletin of the International Union for the Study of Social Insects that later became the journal *Insectes Sociaux*.

specific interactions among individuals were involved in the genesis of certain collective phenomena in insects such as gregariousness in locusts, closure of the colony in many ant species, caste regulation in termites, bee dances, and so on. Pierre-Paul Grassé (see Figure 1) and his students were the first to provide a synthetic view of such collective phenomena that combined both the specificity of interactions among social individuals and organized collective behavior at the colony level. Grassé's basic idea was that sociality is not a trivial consequence that results from interattraction, but a biological characteristic deeply rooted in the ethological heritage of every species. This becomes obvious if one considers the reactions of a social animal in the presence of one of its nestmates: Even if this animal is alone its behavior is different from that of a solitary animal. A social animal displays what Grassé called a *social appetition* that drives it to seek its nestmates. Such a social dependence may prevent this animal from behaving in a normal way when it is isolated and it may even be unable to survive outside a social environment, which is the case, for instance, in bees. Another consequence of interindividual stimuli is what has been called *group effect* [24, 25]. It describes the fact that when an animal is submitted in certain conditions to a critical number of specific stimuli from its nestmates, its behavioral state is altered. Group effect not only involves a stimulus-response sequence, it also leads to a deep change in the reactional state of the animal and sometimes of its whole physiology. One of the most spectacular examples of group effect is the gregarious phase of locusts resulting from stimulus exchanges [7].

Moreover, since a critical number of interactions is reached in an animal society, integrative and regulatory processes emerge. This idea was developed by Grassé who called *social regulation* the fact that a society is able to re-establish a population equilibrium that has been broken or to coordinate the collective performance of a given task through psychophysiological and psychomotor mechanisms. Such a regulation is a social property that results from idiosyncratic features of individual behavior. These mechanisms rely on stimulus-response sequences in which a stimulus is an action performed by one individual and the response another action that has been triggered by this previous action. Each individual is a direct source of stimuli for the other individu-

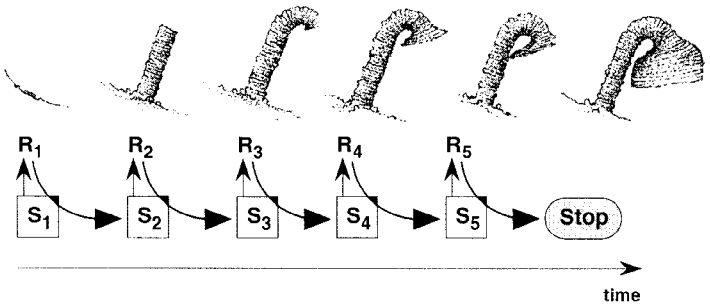


Figure 2. Stimulus-response sequence leading to the construction of the mud funnel in the nest of the Eumenid wasp *Paralastor* sp. Each new building stage n is completed after a stimulus S_n triggers a new ensemble of building actions R_n. The completion of each building stage n gives rise to a new stimulus S_{n+1} that triggers new building actions R_{n+1} leading to the construction of the next building stage $n + 1$. When the fifth stage has been completed, there exists no more stimulus on the funnel to trigger new building actions and the construction stops.

als. This mechanism opens the way for an indirect coordination of individual activities. The processes that regulate such interactions are not limited to the direct influence of the stimuli produced by individuals. Indeed, each animal's activity is organizing the environment in such a way that stimulating structures are created; these structures can in turn direct and trigger a specific action from any other individual from the same species that comes into contact with them. Chemical trails that are produced by some ants species [10, 23], muleteer trail networks, and even dirt tracks and trail systems in man [31, 32] result from interactions of this kind.

One of the most interesting examples studied by Grassé is the building behavior of termites. Stigmergy (from the Greek *stigma*: sting and *ergon*: work) was initially introduced to explain indirect task coordination and regulation in the context of nest reconstruction in termites of the genus *Bellicositermes* [26, 28]. Grassé showed that the coordination and regulation of building activities do not depend on the workers themselves but are mainly achieved by the nest structure: A stimulating configuration triggers a building action 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. Stigmergy offers an elegant and stimulating framework to understand the coordination and regulation of collective activities. The main problem is then to determine how stimuli are organized (in space and time) to generate robust and coherent patterns: Colonies of a given species produce qualitatively similar patterns, be they nest architectures or networks of foraging trails and galleries.

2.4 From Sequential to Stigmergic Activity

To better understand how multiple, "independent" building actions can be coordinated through a stigmergic behavioral algorithm, it is instructive to look at nest construction in solitary species. The experiments performed by Smith in 1978 on a solitary wasp shed some light on the origin of coordination of building activities and on the preadaptation (to sociality) of this behavior [41]. Nest construction in the Eumenid wasp *Paralastor* sp. occurs as a stimulus-response sequence in which the completion of one stage provides the stimulus for commencement of the next (see Figure 2). A wasp begins with the excavation of a narrow hole, approximately 8 cm in length and 8 mm in width. When the nest hole has been completely lined with mud, the wasp begins the construction of a large and elaborate mud funnel above its entrance. The funnel is built in five distinct stages from a series of mud pellets that are applied in a

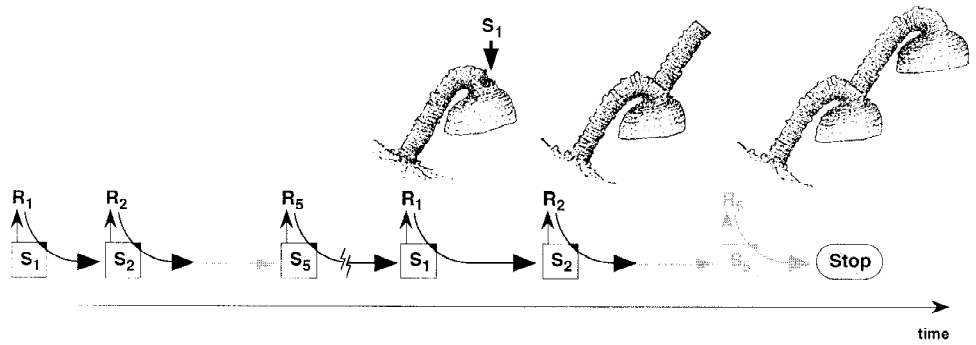


Figure 3. The construction of an abnormal mud funnel in the nest of the Eumenid wasp *Paralastor* sp. When the funnel is almost completed, a spherical hole (indicated by the arrow) is made. This hole is equivalent to stimulus S_1, which triggers funnel construction. As a consequence, the wasp builds a second funnel, over the hole and on top of the first one already built.

highly stereotyped sequence. Stage 1 involves the building up of the funnel stem by application of a series of mud pellets until it reaches a length of 3 cm. At Stage 2 the wasp ceases to build uniformly upward, and by adding more mud to one side begins the construction of a uniform curve in the stem of the funnel. Once the curve has been completed, Stage 3 begins with the formation of a bell with the splaying of the stem to form a uniform flange of approximately 2 cm diameter. At Stage 4, the flange is next widened more on the side nearest to the stem than elsewhere, thus giving the bell a characteristic asymmetry in one direction. Finally at Stage 5, the sides of the bell are formed by building uniformly downward from the edge of the flange. At the end of each stage of building, the stimuli for the responses that lead to the completion of the next stage are those that the animal encounters as a consequence of its earlier behavior. What happens when the stimuli that trigger the beginning of a previous building stage are encountered by the wasp just as it finishes the end of a particular stage? Smith examined this question in one of his experiments. A spherical hole located in the neck of a funnel is made just after Stage 3 has been completed (see Figure 3). After examining the damage several times, the wasp begins the construction of a second funnel, over the hole and on top of its first funnel. This result is extremely important for anyone who wants to understand the coordination of building activities in social wasps and more generally in social insects. In a solitary species such as *Paralastor* sp., the indirect coordination of its behavior through the previous consequences of its building actions results in a sequential-like behavior. There are two consequences to this behavior.

First, the order in which stimuli arise in the course of the construction must follow a precise sequence. If by chance a stimulus triggering a set of building actions that gives rise to a previous subelement of the architecture is present at a later stage, this will automatically lead to a redundant structure and an abnormal nest architecture. This observation, as we will see in the next section, has important consequences in the coordination of building activity in social wasps.

Second, if one wasp does not distinguish the product of its own activity from that of another wasp, the two wasps can in principle work at completing the same nest structure. One wasp could continue the work of the other at whatever stage of construction of the nest. Such a mechanism may then in turn be a step toward indirect cooperation between individuals. This is precisely the mechanism that Grassé had in mind when he introduced the concept of stigmergy.

3 Stigmergy Revisited

Stigmergy refers to a class of mechanisms that mediate animal-animal interactions. Therefore, it has to be supplemented with an additional mechanism that makes use of these interactions to coordinate and regulate collective building in a particular way. At least two such mechanisms have been identified: quantitative stigmergy [1, 9, 11] and qualitative stigmergy [43, 44]. With quantitative stigmergy, the stimulus-response sequence comprises stimuli that do not differ qualitatively (such as pheromone fields and gradients) and only modify the probability of response of the individuals to these stimuli. Qualitative stigmergy differs from quantitative stigmergy in that individuals interact through, and respond to, qualitative stimuli.

3.1 Quantitative Stigmergy and Self-Organized Dynamics

One of the best examples of quantitative stigmergy is the construction of pillars in termites, studied by Grassé [26, 28]. Workers use soil pellets impregnated with pheromone to build pillars. Two successive phases take place [26]. 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 attractiveness of deposits through the diffusing pheromone emitted by the pellets ([5]; see Figure 4). 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 illustrates three important properties or signatures of the self-organized dynamics associated with quantitative stigmergy [1]: (a) the emergence of spatiotemporal structures in an initially homogeneous medium, that is, a random spatial distribution of soil pellets. The basic mechanism that leads to the emergence of these structures is positive feedback (the snowball effect); once the structures are created, they are stabilized through negative feedback, mainly pheromone decay and competition among neighboring pillars. (b) 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). (c) the existence of (parameter-driven) bifurcations, where the behavior of a self-organized system changes dramatically. In 1977, Deneubourg ([8], see also [2]) designed a chemotaxis-based reaction-diffusion model of the emergence of regularly spaced pillars in termites that exhibits the desired properties for appropriate parameter values. Figure 5 shows the one-dimensional spatial distribution of pillars obtained with his model. In this example, coordination between workers and the regularity of the pillars' distribution emerges out of indirect interactions among termites without being coded in an explicit way at the level of each insect.

3.2 Qualitative Stigmergy and Self-Assembling Dynamics

3.2.1 Qualitative Stigmergy

Qualitative stigmergy differs from self-organization-based stigmergy in that individuals interact through, and respond to, *qualitative* stimuli. The resulting dynamics is similar to that resulting from a self-assembling process. Qualitative stigmergy is based on a discrete set of stimulus types: For example, an insect responds to a type-1 stimulus with

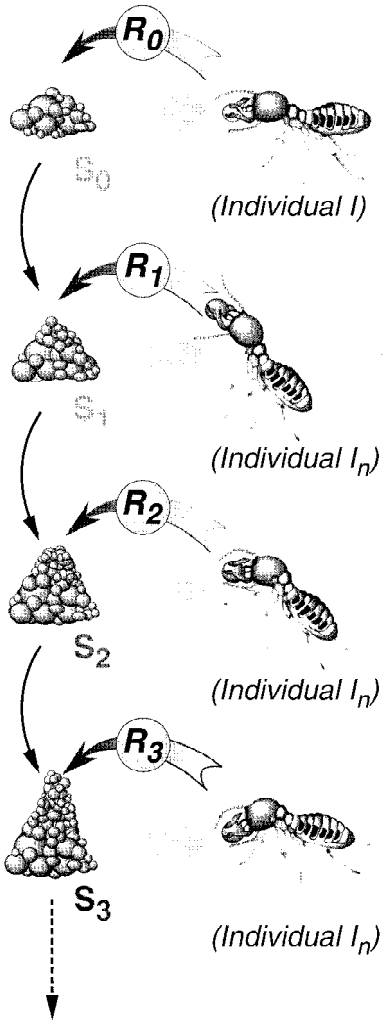


Figure 4. Schematic representation of quantitative stigmergy illustrated by the successive stages leading to the emergence of pillars in termite nests. To build their nest termite workers use soil pellets impregnated with pheromone. The existence of an initial deposit of soil pellets stimulates workers 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. Assume that the architecture reaches state S_0, which triggers response R_0 from worker I. S_0 is modified by the action of I (e.g., I drops a new soil pellet) and transformed into a new stimulating configuration S_1, which may in turn trigger a new response R_1 from I or any other worker I_n, and so forth. The successive responses R_1, R_2, R_n may be produced by any worker carrying a soil pellet. Each worker creates new stimuli in response to existing stimulating configurations. In this example, the successive stimuli differ from one another only in the quantity of pheromone that is present on the pillar. This example therefore illustrates positive feedback in quantitative stigmergy.

action A and responds to a type-2 stimulus with action B, in the same way that the mud wasp *Paralastor* builds the funnel of its nest. In other words, qualitatively different stimuli result in different responses: 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. At first sight, it is unclear how coordination and regulation can be achieved with qualitative stigmergy. Building in social wasps provides a good illustration (Figure 6) of how this can work.

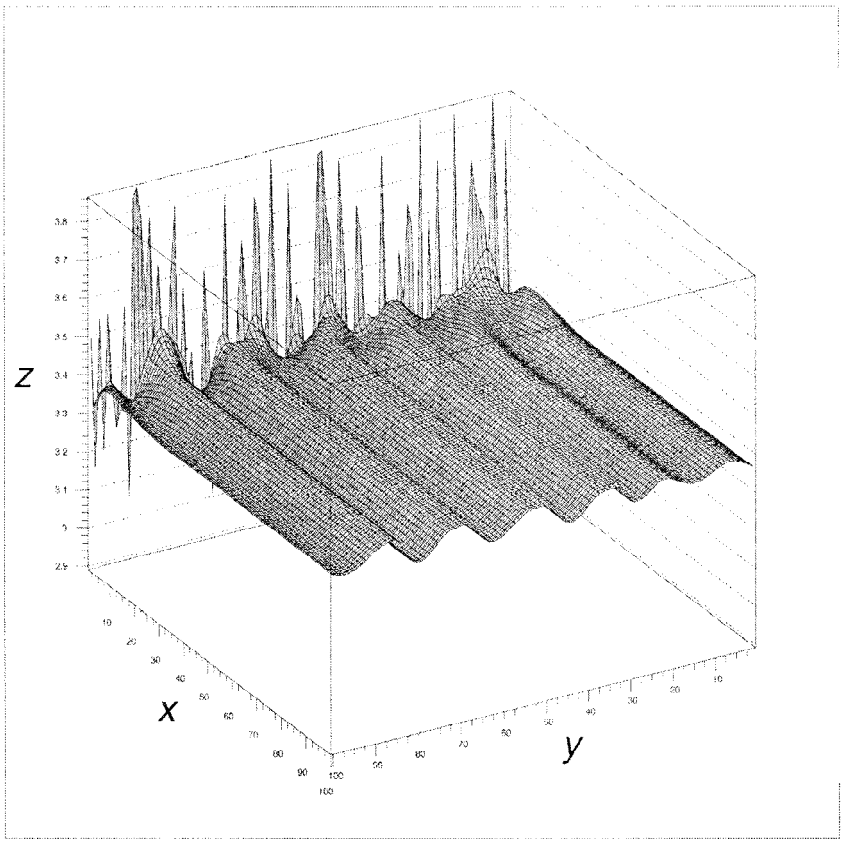


Figure 5. Spatial distribution of soil pellets obtained from Deneubourg's [8] model in one dimension [2]; x: time, y: space, z: quantity of building materials.

3.2.2 Building in *Polistes*

One example is nest building in the primitively eusocial wasp *Polistes*. The article by Karsai in this special issue gives a detailed overview of stigmergic procedures used by paper wasps to build their nests. *Polistes* use long wood fibers and plant hairs that are mixed with salivary secretions. The resulting carton is easily shaped and has a strong robustness though it is extremely fine and light [29]. A nest consists of a single comb connected to the substrate by a rodlike pedicel [45]. The comb is round shaped and mature nests can contain about 150 cells [39]. New cells are added to the comb during nest growth and the number of potential sites where a new cell can be added increases as construction proceeds. Several building actions may take place in parallel. However, this raises the question of where new cells are to be added to get a nest architecture that is species-specific. Due to the possibility of parallel activities, another problem arises: Construction may become messy as conflicting actions may be performed simultaneously.

These two issues are connected and the architecture itself provides enough constraints to canalize the building activity and prevent its deorganization. Let us consider the comb shown in Figure 7, with six cells already built; twelve potential building sites can be found on this comb: seven sites with one wall already present (labeled S_1), four sites with two adjacent walls (S_2), and one other site with 3 adjacent walls (S_3). Figure 8 shows how the mean number of potential building sites (with either 1, 2, or

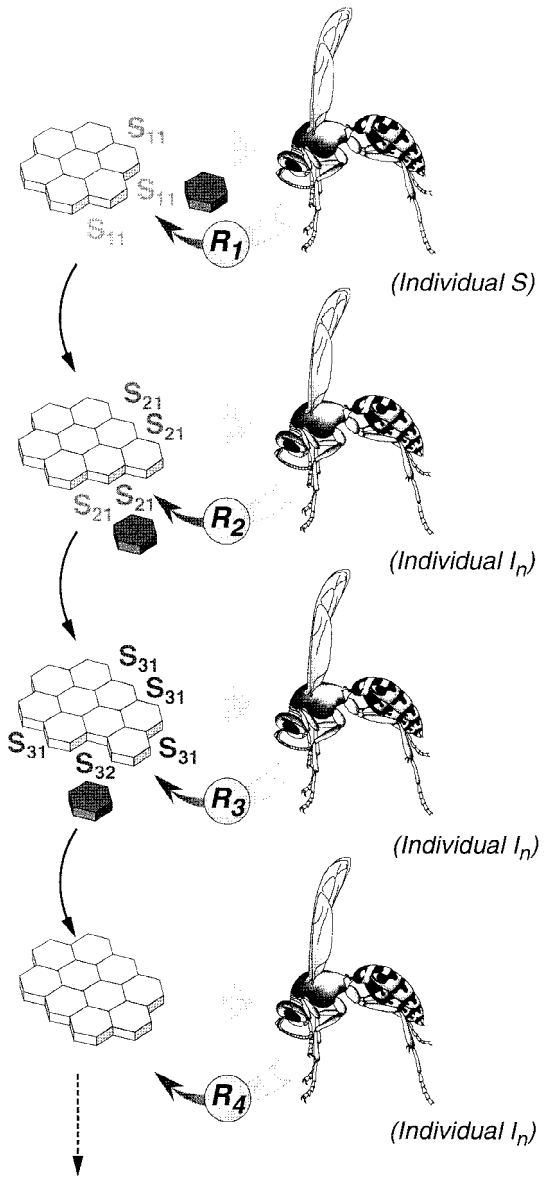


Figure 6. Schematic representation of qualitative stigmergy illustrated by the successive stages leading to the construction of a comb in wasps. The wasps use wood pulp to build the various elements of their nest. Here, each building stage corresponds to the addition of a new cell to the pre-existing comb. At the beginning (top of the figure) all potential building sites are equivalent. Each one of them (S_{11}) has two adjacent walls. No construction is observed on the six other sites that have only one wall. The building of the new cell (R_1) by wasp I results in the creation of a new potential building site with two walls, but all building sites (S_{21}) remain equivalent from a qualitative point of view. The addition of a second cell to the comb (R_2) produces building site (S_{32}) that has three adjacent walls and is qualitatively different from the others (S_{31}). Each wasp I_n creates new qualitative stimuli in response to existing stimulating configurations. Successive stimuli differ from one another in their spatial configurations of external walls.

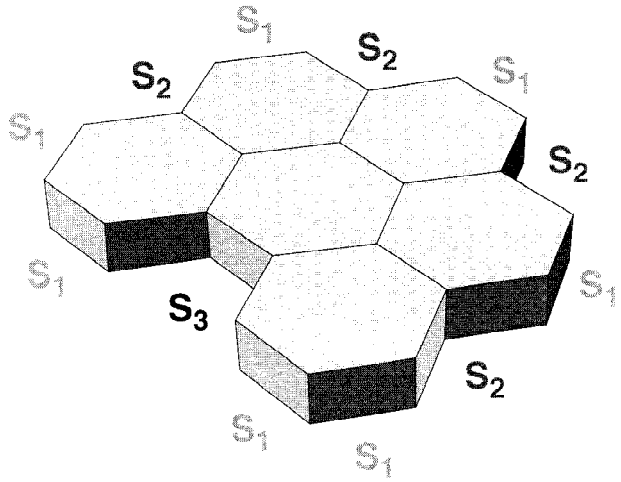


Figure 7. Representation of the potential building sites that have one (S_1), two (S_2), or three (S_3) walls in common with the new cell added to the comb.

3 adjacent walls) varies as a function of the number of cells already built in the comb. Since it appears that the growth of the comb is isotropic, that is, it occurs with equal probability in all directions of space, the question that arises is: How are cells added to ensure that the comb will grow fairly evenly in all directions from the pedicel? Previous studies showed that wasps are obviously influenced by previous construction, and that building decisions are made locally on the basis of perceived configurations in a way that possibly constrains the building dynamics (see also the article by Karsai in this issue). Cells are not added randomly to the existing structure and 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 [12, 34]. One building rule is that wasps tend to finish a row of cells before initiating a new row. Figure 9 shows that the probability to add a cell to a three-wall site is about 10 times higher than in the case of a two-wall site. What are the consequences of this probabilistic stigmergic behavior on the development of the comb structure?

3.2.3 Lattice Swarms

In a series of previous articles we introduced a class of models to explore the potential of qualitative stigmergy as a model of nest construction [43, 44]. The models are based on asynchronous automata that perform random walks in a three-dimensional discrete space, have access to local space and time information, and act on a pure stimulus-response basis: A set of builders (automata, agents or artificial wasps) move in three dimensions and respond to particular stimuli present on the developing comb structure. The three-dimensional space in which the automata move is a discrete cubic or hexagonal lattice—hence the name lattice swarms. The deposit of an elementary building block, or brick, by an agent depends on the local configuration of bricks in the cells surrounding the cell occupied by the agent (see Figure 10). Several types of brick can be deposited, and no brick can be removed once it has been deposited. Increasing the number of brick types increases the repertoire of local configurations that are perceived by the agents. In the simulations reported below two types of bricks were used, which is the minimal number of types with which "complex" patterns can be generated. All simulations start with a single initial brick. A microrule is defined as the association of a particular stimulating configuration and a brick to be deposited.

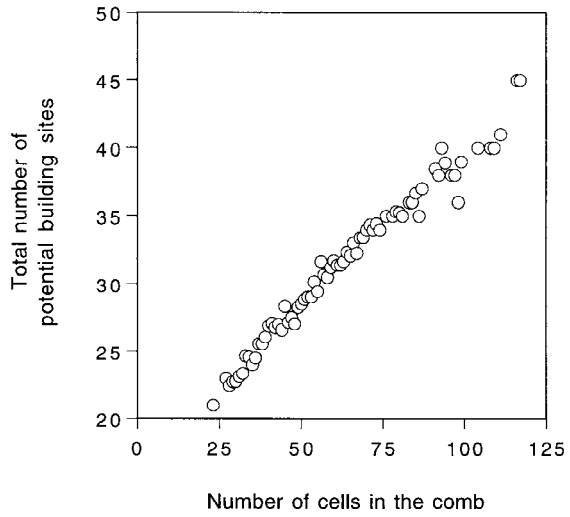


Figure 8. Mean number of potential building sites with 1, 2, and 3 walls adjacent to the new cell as a function of the number of cells already built in the comb in *Polistes dominulus*. The curve is based on 155 mesures made on 13 colonies reared in laboratory conditions and observed at various stages of development.

Two microrules are incompatible if they have the same stimulating configuration but command different actions, here the deposits of different bricks. An algorithm is defined as any collection of compatible microrules: It consists of a set of if-then rules, in which the "if" statement tests for a particular configuration of bricks in the structure, and the "then" statement results in the deposition at that site of one of the two types of bricks. An algorithm can be characterized by its microrule table, a lookup table comprising all its microrules, that is, all stimulating configurations and associated actions. Finally, an algorithm can be deterministic or probabilistic: If it is deterministic any applicable

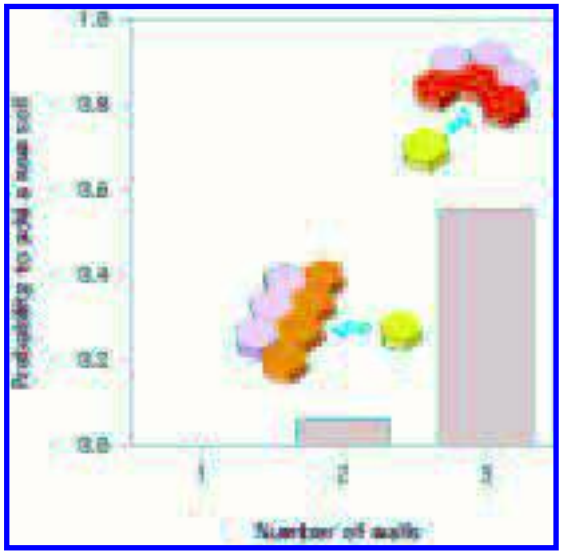


Figure 9. Probability of adding a new cell at sites that have 1, 2, and 3 walls adjacent to the potential new cell.

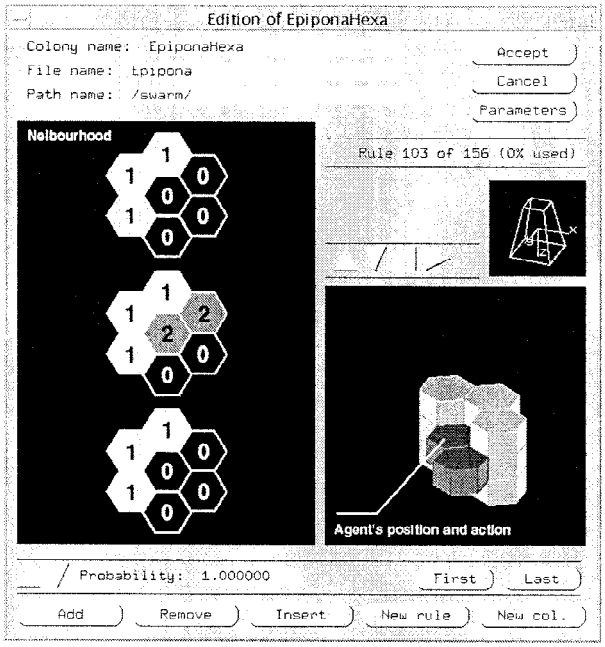


Figure 10. Schematic representation of an agent's perception range in a hexagonal lattice. Each one of the 20 neighboring cells can either be empty or contain either a type-1 brick or a type-2 brick. Each local configuration can be associated with a building action, that is, a brick deposit. There exist $3^{3^{20}}$ possible elementary microrules, and the building behavior of an agent relies on several microrules.

microrule is applied with probability 1; in the second case, a probability between 0 and 1 is assigned to each microrule.

Lattice swarms can be used to study the dynamics of comb enlargement in *Polistes* wasps. Comb structures produced with deterministic and probabilistic algorithms can easily be compared. We shall consider only the two following rules (see Figure 11):

Rule 1: Add a new cell at a two-wall site location.

Rule 2: Add a new cell at a three-wall site location.

In the first simulation, both rules are applied every time an agent encounters the right stimulating configuration. In the second case, rules are applied with the experimental probabilities found in natural *Polistes* colonies: respectively 0.057 for Rule 1 and 0.55 for Rule 2. Figure 12a shows a comb that has been obtained using deterministic rules. The comb is indented in many places, with several lobes. On the other hand, using probabilistic rules leads to the construction of a round-shaped comb similar to what is found in natural *Polistes* nests (Figure 12b). Similar results have been obtained by Karsai and Pénzes [33]. These differences can be simply explained by the fact that in the probabilistic rule, three-wall sites trigger cell building with a higher probability; this process results in building closely packed parallel rows of cells and the nest grows fairly evenly in all directions.

Using lattice swarm models, it is possible to build much more complex architectures [43, 44]. Figure 13 shows a few architectures that have been obtained using deterministic rules in cubic and hexagonal environments. According to their neighborhoods and lookup tables, agents may put down two types of brick (type 1 or type 2). Al-

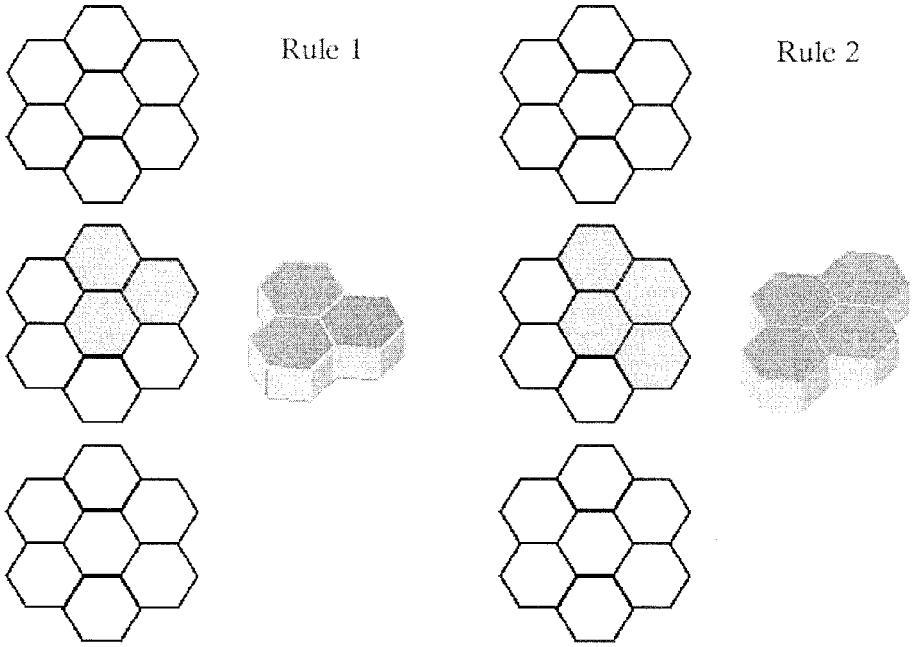


Figure 11. Two local microrules used to build the comb of a *Polistes*-like nest.

though the underlying behavioral principle is quite simple, complex architectures can form, some of which closely match those found in nature. Future work will be aimed at verifying that such complex architectures can still be produced with probabilistic algorithms.

4 Conclusions

The basic principle of stigmergy is extremely simple: Traces left and modifications made by individuals in their environment may feed back on them. The colony records its activity in part in the physical environment and uses this record to organize collective behavior. Various forms of storage are used: gradients of pheromones, material structures (impregnated or not by chemical compounds), or spatial distribution of colony elements. Such structures materialize the dynamics of the colony's collective behavior and constrain the behavior of individuals through a feedback loop. Stigmergy also solves the coordination paradox: Individuals *do* interact to achieve coordination but they interact indirectly, so that each insect taken separately does not seem to be involved in a coordinated, collective behavior.

As a consequence of the medium used, physical and geometrical constraints influence subsequent choices of the colony. It is well known that in ant species using mass recruitment, when several food sources are discovered independently, the closest source to the nest is selected by the colony [23]. Indeed when the distance between a food source and the nest is long, the time interval between the trips of two foragers may exceed the evaporation latency of the pheromone and the trail disappears. If the path is shorter, the traffic is sufficiently intense for the pheromonal trace to remain. This dynamic improves the exploitation of the environment by the colony. An interesting property of this process is that various organizations may be produced with the same individual behavioral algorithms: Several foraging patterns can be produced according

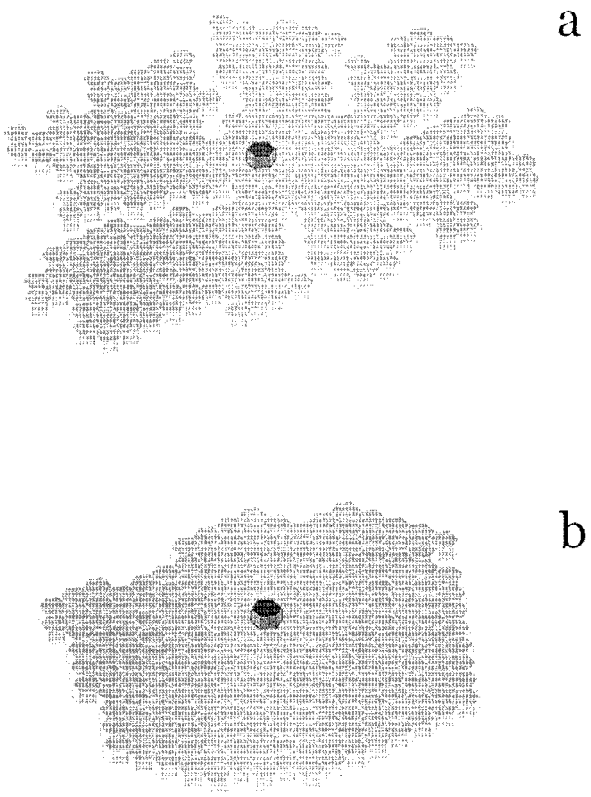


Figure 12. (a) Comb structure obtained when deterministic rules are used. (b) Comb structure obtained when probabilistic rules are used.

to the distribution of resources, as illustrated by army ants [10]. Similar coupling between environmental and social organization may be found in the self-organization of brood patterns in bees and ants. In a bee hive (*Apis mellifica*), the comb is organized in three concentric regions of cells: a central brood area, a rim of pollen, and a peripheral zone of honey. It has been shown using computer simulation that such patterns may arise spontaneously from the dynamics of interactions, according to behavioral rules bearing only upon local cues [6]. In lepthoracin ants, eggs, larvae, and cocoons are sorted out by workers according to their developmental stage. A model worked out by Deneubourg et al. [11] showed that this structuration may arise from a tendency of workers to deposit brood elements on heaps of the same category, in a positive feedback loop similar to those reported in termites.

Marking the environment with glandular secretions, urine, or feces has been reported in a number of mammals, the scent-mark of an individual frequently inducing remarking by others [4]. Besides the function of advertising conspecifics, marks may help individuals orient themselves in their range [see 3, 22, 30, 40]. Though scent-marks can be used as reminders by individuals, they should not be viewed only as landmarks: They are actually part of the environmental structure and contribute to its definition. In species forming social groups, marking is a collective affair; chemical signals are deposited throughout the range, their distribution being denser at much-visited sites such as junctions, dens, or zones where individuals from other groups may be encountered [4]. Group members continuously come across olfactory signals; they obtain informa-

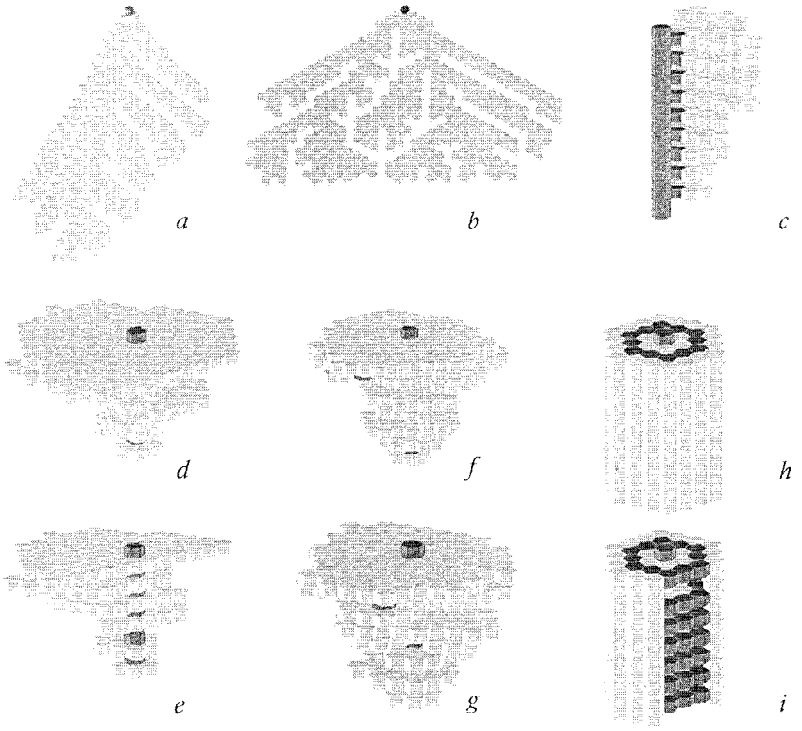


Figure 13. Simulations of collective building on a 3D cubic (a) and hexagonal (b to i) lattice. Simulations were run with a $40 \times 40 \times 40$ lattice for architectures a and b; with a $20 \times 20 \times 20$ lattice for architecture c; and with a $16 \times 16 \times 16$ lattice for architectures d to i. These architectures are reminiscent of natural wasp nests and exhibit a similar design. For each architecture we give the name of the corresponding natural wasp nest species and in brackets the total number of microrules used to build it. (a) *Agelaia* nest-like architecture (13). (b) *Parapolybia* nest-like architecture (12). (c) *Parachartergus* nest-like architecture (21). (d) *Vespa* nest-like architecture (13). (e) Same architecture as (d) shown in front section. (f, g) *Stelopolybia* nest-like architectures (12). (h) *Chartergus* nest-like architecture (39). (i) Same architecture as (h) but a portion of the external envelope has been partly removed to show the internal structure of the nest.

tion about each other's movements that may improve foraging efficiency and maintain group cohesion [3, 13, 21].

Stigmergy also has consequences with respect to the evolution of social life, and the route from solitary to social life might not be as complex as one may think. Numerous examples of solitary species that use stigmergy are known: Many solitary animals, such as spiders [36], are not able to see the differences that exist between the products of their own activities and those of conspecifics. Occasional cooperation between conspecifics may spontaneously emerge in these "preadapted-to-social-life" species if, by accident, they find themselves in the same location. Of course stigmergy alone is not a sufficient condition to develop a truly social life and two additional features are required that are closely related, yet not exactly identical: a "preadapted" species must be able to reach locally high population density, that is, possess some kind of "homing" mechanism or interattraction allowing cluster formation. The second condition is that once many individuals have joined to form a group, they must be able to maintain its cohesion long enough to benefit from cooperative effects.

In conclusion, the potential of stigmergy is still largely untapped in the biology community, in which it originated. Perhaps, as the other articles in this special issue indicate, the sciences of the artificial will be more open to this potential.

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